Genetic selection for health and welfare traits in lambs

Stephanie M. Matheson

Thesis submitted for the degree of Doctor of Philosophy

The University of Edinburgh

2011

DECLARATION

I declare that this thesis is my own work. Neither this work, nor any part of it, has previously been submitted for any other degree or professional qualification.

S. M. Matheson
December 2011

THESIS ABSTRACT

Lamb mortality remains a significant welfare and economic issue for sheep production. Two significant causes of mortality are dystocia and low lamb vigour; both requiring high levels of human care to ensure lamb survival. Genetic solutions to reduce lamb mortality and its main causes (dystocia and low vigour lambs) are desirable, with at least two possible solutions available: (i) use of suitable breeds or strains and (ii) intrabreed selection. Approach (i) requires the existence of breed/strain differences in the desired traits and approach (ii) needs sufficient intrabreed genetic variance. Reproductive and behavioural traits are, however, difficult to quantify and measure on farm. On dedicated research farms, lamb vigour has been measured using latencies to perform specific behaviours (e.g. standing and sucking) but this methodology is difficult to transfer to a commercial setting - timed behavioural traits are not as easy to measure on farm when compared with categorical indicator traits. Therefore, proxy methods (categorical scoring systems) are needed to measure behaviour traits in a manner that allows for collection of sufficient data to enable genetic analysis. The main purpose of this thesis was to develop such proxy methods, to estimate the heritability of lamb traits, and thus to investigate whether it is possible to improve the welfare of lambs through selection of parents with superior vigour and lambing ease characteristics.

Scoring systems were developed for quantifying neonatal lamb fitness and behaviour traits. Detailed historical behaviour data were analysed to develop criteria for three scores: birth assistance (BA), lamb vigour (LV) and sucking assistance (SA). These scoring systems were then validated in a separate flock by simultaneously recording scores and the latency to perform certain landmark behaviours. The results obtained indicated that the scoring systems developed were a practical, reliable and sensitive indicator of lamb fitness traits. To determine whether neonatal lamb vigour traits were heritable, scores from the scoring systems previously developed and validated were recorded in an experimental flock of pure-bred Texel sheep for the purpose of estimating genetics parameters for each trait. Results indicated that heritabilities for all traits range from low-moderate, BA 0.43 (s.e. 0.063), LV 0.15 (s.e. 0.059), SA (0.27 (s.e. 0.045), suggesting there is sufficient variation present within this Texel sub-population to allow for selection for improved neonatal fitness traits.

Thus far, we have determined that neonatal traits are heritable and can be measured using proxy scoring systems. The next step was to establish whether the proxy scores developed were feasible, in a commercial setting, for the mass data collection needed for estimation of genetic parameters and to determine the relationship between neonatal traits and later production traits, with the aim of integrating this data into breeding programmes. A total of 11,092 lambs with complete neonatal records, from 290 flocks belonging to the Industrial Partner, the Suffolk Sheep Society (UK), were analysed to report the genetic variance present within the UK population of registered pure-bred Suffolk sheep. The results from this analysis show that heritabilities were moderate for BA, 0.26 (s.e. 0.03), LV, 0.40 (s.e. 0.04) and SA, 0.32 (s.e. 0.03) with genetic correlations between neonatal traits all moderate to high and positive. This demonstrates that neonatal fitness traits can have heritabilities comparable to those of production traits. The analysis also shows that neonatal survival traits of birth assistance and sucking assistance are moderately heritable, when treated as a lamb trait rather than a sire or ewe trait, indicating the selection should target the lambs in order to successfully, and efficiently, improve survival.

A possible alternative method for improving dystocia and lamb vigour would be to introgress genes for improved lambing ease and lamb vigour from the New Zealand strain of Suffolk sheep into the British Suffolk strains. However, there has been no published record of how much ‘NZ genetics’ would improve (or compare to) British Suffolk’s under standard UK management practises. Therefore, the objectives of this study were to examine possible differences in neonatal behavioural traits (birth assistance, lamb vigour and sucking assistance) between NZ and UK Suffolks when used as terminal sires on commercial cross-bred ewes. Thus, neonatal scores from cross-bred lambs sired by rams from one of the three main Suffolk strains currently used in the UK were compared. The analysis indicated there was no significant effect of sire strain on any of the neonatal traits, and that individual sire variation was greater than the variation between the strains.

In conclusion, the work contained within this thesis shows that neonatal lamb behaviour traits can be measured accurately and easily using well-realised and biologically relevant scoring systems. Furthermore, these scoring systems are a feasible and practical method of measuring neonatal lamb vigour which may be used to evaluate management systems and to improve selection criteria for neonatal traits.

ACKNOWLEDGEMENTS

During the course of this PhD I have met many interesting people, and I would like to take this opportunity to thank some of them. I would like to express my thanks and gratitude for my supervisors – Prof. Cathy Dwyer, Dr Lutz Bünger and Dr Jos Houdijk – who can all be heard heaving a sigh of relief. Thanks guys, your comments on my manuscripts will be forever taped to the wall.

My gratitude also goes to Dr John Vipond and Dr John Rooke. Who both mothered me around my first conference and read various bits of text. These are also the people who called me ‘untame’, ‘bolshy’ and ‘retarded’. Thanks.

I would like to thank my funding body, the BBSRC, and my Industrial Sponsor, the Suffolk Sheep Society, for funds and access to some of the data needed for this thesis. My gratitude goes to the Worshipful Company of Woolmen for the award that allowed me to present my work at various conferences. I’d also like to acknowledge the part that various tea companies and McVitie’s dark chocolate digestives have played throughout the last few years.

For my friends and colleagues who have shared my moods, thanks. There are many of you but special mention goes to Jenny Howie, Dagmar Kapell, Laszlo Trefan, Alice Barrier and Jill Mackay.

The two most important people to thank are: my mother, for always telling me that I should enjoy what I do, and to Davor, for just … well … just.

I had a lot of fun during the course of this PhD. All that I can say is thanks.

REFEREED PUBLICATIONS:

Chapter two has been published:

MATHESON, S.M., J.A. ROOKE, K. MCILVANEY, M. JACK, S. ISON, L. BÜNGER & C.M. DWYER 2011 Development and validation of on-farm behavioural scoring systems to assess birth assistance and lamb vigour. Animal 5 (5): 776-783.

Chapter three has been submitted:

MATHESON, S. M., J. RODEN, W. HARESIGN, L. BUNGER and C. M. DWYER, 2010 Lambing ease and lamb vigour characteristics in lambs sired by rams of three main Suffolk strains. Submitted to Small Ruminant Research.

Chapter four will be submitted:

MATHESON, S.M., C.M. DWYER, J.M. MACFARLANE, W. HARESIGN, N.R. LAMBE & L. BUNGER. Genetic parameters for birth assistance and lamb vigour traits in a pure-bred Texel population accounting for Texel double-muscling QTL (TM-QTL) genotypes. Will be submitted to either Behavior Genetics or Journal of Animal Science.

Chapter five has been submitted:

MATHESON, S.M., L. BUNGER & C.M. DWYER. Genetic parameters for fitness and neonatal behaviour traits in sheep. Submitted to Behavior Genetics.

CONFERENCE PUBLICATIONS:

MATHESON, S. M., J. M. MACFARLANE, L. BUNGER and C. M. DWYER 2010 Genetic parameters for neonatal lamb traits in Suffolk sheep. Session 10, no. 4, p84. in: *Proceedings of the 44th Congress of the International Society for Applied Ethology (ISAE), Uppsala, Sweden.*

MATHESON, S.M., L. BUNGER, C.M. DWYER and J.G.M. HOUDIJK 2010 Relationship between neonatal lamb vigour and faecal soiling at weaning in lambs. p57. In: *Proceedings of the 14th International Conference on Production Diseases in Farm Animals, Ghent, Belgium*.

MATHESON, S.M., J. RODEN, W. HARESIGN, L. BUNGER and C.M. DWYER, 2010 Selection of sires with good lambing and lamb vigour characteristics within three Suffolk strains. p170. In: *Proceedings of the British Society of Animal Science, Belfast, Northern Ireland.*

MATHESON, S.M., C.M. DWYER, L. BUNGER and J.G.M. HOUDIJK, 2010 Interactions between neonatal lamb vigour and faecal soiling at weaning in three breeds of sheep. p226. In: *Proceedings of the British Society of Animal Science, Belfast, Northern Ireland.*

Posters:

MATHESON, S.M. & C.M. DWYER, 2008 Welfare assessment of neonatal lambs. p139. In: *Proceedings of the 4th International Workshop on the assessment of Animal Welfare at Farm and Group Level, Ghent, Belgium*.

TABLE OF CONTENTS

DECLARATION II
THESIS ABSTRACT III
ACKNOWLEDGEMENTS VI
REFEREED PUBLICATIONS: VII
CONFERENCE PUBLICATIONS: VIII
TABLE OF CONTENTS IX
CHAPTER ONE 1
GENERAL INTRODUCTION 1
1.1 LAMB MORTALITY 2
1.2 DEFINITION OF LAMB VIGOUR 3
1.3 CONSEQUENCES OF POOR LAMB VIGOUR 3
1.4 MANAGEMENT INTERVENTIONS TO REDUCE LAMB MORTALITY 5
1.4.1 Human assistance at parturition 5
1.4.2 Nutritional supplementation 7
1.5 BREEDING FOR GENETIC IMPROVEMENT 9
1.5.1 Maternal trait selection for reproductive traits 10
1.5.2 Direct selection to reduce lamb mortality 12
1.6 HOW CAN NEONATAL BEHAVIOUR TRAITS BE QUANTIFIED? 14
1.7 THESIS AIMS 17
1.8 THESIS OUTLINE 18
CHAPTER TWO 20
DEVELOPMENT AND VALIDATION OF ON-FARM BEHAVIOURAL SCORING SYSTEMS TO ASSESS BIRTH ASSISTANCE AND LAMB VIGOUR 20
2.1 ABSTRACT 21
2.2 IMPLICATIONS 23
2.3 INTRODUCTION 23
2.4 MATERIALS AND METHODS 25
2.4.2 Study 2: Validation of the Scoring Systems 28
2.5 RESULTS AND DISCUSSION 29
2.5.1 Study 1: Development of the Scoring Systems 29
2.5.2 Study 2: Validation of the Scoring Systems 36
2.5.3 Sensitivity of the Scoring Systems 38
2.5.4 Effectiveness of scoring systems as selection criteria 41
2.5.5 Use of Scores in Commercial Farm Situations 41
2.6 GENERAL IMPLICATIONS 42
2.7 CONCLUSIONS 42
CHAPTER THREE 43
LAMBING EASE AND LAMB VIGOUR CHARACTERISTICS IN LAMBS SIRED BY RAMS OF THREE MAIN SUFFOLK STRAINS 43
3.1 ABSTRACT 44
3.2 IMPLICATIONS 45

3.3 INTRODUCTION 45
3.4 MATERIAL AND METHODS 47
3.4.1 Animals 47
3.4.2 Statistical methods 50
3.5 RESULTS 51
3.5.1 Sire strain analysis 51
3.5.2 Fixed effects on neonatal scores 53
3.6 DISCUSSION 55
3.7 CONCLUSIONS 57

CHAPTER FOUR 58

GENETIC PARAMETERS FOR BIRTH ASSISTANCE AND LAMB VIGOUR TRAITS IN A PURE-BRED TEXEL POPULATION ACCOUNTING FOR TEXEL DOUBLE MUSCLING QTL (TM-QTL) GENOTYPES 58

4.1 ABSTRACT 59
4.2 INTRODUCTION 60
4.3 MATERIALS AND METHODS 62
4.3.1 Animals 62
4.3.2 Ewe and lamb management 62
4.3.3 Data collection 63
4.3.4 Statistical analysis 65
4.4 RESULTS 66
4.4.1 TM-QTL Genotype analysis 66
4.4.2 Fixed effects on neonatal behaviour scores 67
4.4.3 Genetic parameters 70
4.5 DISCUSSION 71
4.5.1 TM-QTL Genotype 71
4.5.2 Fixed effects 72
4.5.3 Genetic parameters 73
4.6 CONCLUSION 75

CHAPTER FIVE 76

GENETIC PARAMETERS FOR FITNESS AND NEONATAL BEHAVIOR TRAITS IN SUFFOLK SHEEP 76

5.1 ABSTRACT 77
5.2 INTRODUCTION 78
5.3 MATERIALS AND METHODS 80
5.3.1 Animals 80
5.3.2 Data collection 80
5.3.3 Statistical analysis 83
FYG^2 83
5.4 RESULTS AND DISCUSSION 84
5.4.1 Neonatal traits and performance recording 84
5.4.2 Fixed effects on neonatal and production traits 86
5.4.3 Behavioral genetics 94
5.5 CONCLUSION 102

CHAPTER SIX 103

INTERACTIONS BETWEEN NEONATAL BEHAVIOUR TRAITS AND FAECAL SOILING AT WEANING IN THREE BREEDS OF SHEEP 103

6.1 ABSTRACT 104
6.2 INTRODUCTION 105
6.3 METHODS AND MATERIALS 106
6.3.1 Animals 106

6.3.2 Statistics *109*
6.4 RESULTS 110
6.4.1 Breed, lamb sex, litter size and birth weight effects *110*
6.4.2 Relationship between neonatal traits and weaning traits *112*
6.4.3 Relationship between faecal soiling, live weight at weaning and growth rate *115*
6.5 DISCUSSION 115
6.5.1 Breed, lamb sex, litter size and birth weight effects *116*
6.5.2 Lamb vigour – sucking ability – faecal soiling relationship *117*
6.6 CONCLUSION 120

CHAPTER SEVEN 121

GENERAL DISCUSSION 121

7.1 CHAPTER SUMMARIES 122
7.2 GENERAL DISCUSSION 124
7.3 IMPACT OF GENETIC CHANGE 129
7.4 EARLY DEVELOPMENT AND HEALTH TRAITS AT WEANING 131
7.5 FUTURE DIRECTIONS 132
7.6 CONCLUSIONS 134

APPENDIX I 135

APPENDIX II 138

APPENDIX III 142

REFERENCES 145

CHAPTER ONE

GENERAL INTRODUCTION

1.1 Lamb mortality

Lamb mortality is a significant welfare and production issue for the sheep industry (ALEXANDER 1988; HAUGHEY 1993). Worldwide estimates suggest that 15-30% of lambs die before weaning, with mortality rates highest within the first 3 days of postnatal life (NOWAK *et al.* 2000; SAWALHA *et al.* 2007; BRIEN *et al.* 2010). Lamb production is an important economic trait (LOPEZ-VILLALOBOS and GARRICK 1999), with lamb survival one of the major influences on overall productivity in the UK (CONINGTON *et al.* 2004). Lamb mortality can be interpreted as being a welfare indicator within the flock (WATERHOUSE 1996) and from a welfare point of view, it is important to recognise that a large proportion of these losses are avoidable (GODDARD 2011).

Dystocia, an abnormal or difficult birth, has been reported to be one of the primary causes of mortality within 3 days after birth (KERSLAKE *et al.* 2005), due to either an abnormal presentation or a disproportion between the ewe's pelvis and the lamb's head and it can reduce lamb vigour (HINCH *et al.* 1985). Other causes of mortality include hypothermia (MELLOR 1983; MELLOR 1988), placental insufficiency (MELLOR 1983; MELLOR 1988), starvation (EALES and SMALL 1981; MELLOR and COCKBURN 1986), maternal undernutrition (MELLOR 1983; MELLOR and COCKBURN 1986; MELLOR 1988), mismothering (FRASER and BROOM 1998) and infections (CAMPBELL *et al.* 1977). Accordingly, dystocia and poor lamb vigour (lambs which are slow to stand) are significant contributors to lamb mortality, along with poor maternal care, infection and starvation/hypothermia.

Lamb survival is, to a degree, dependent upon an easy delivery and the expression of appropriate behaviours from both mother and offspring – such as rapid standing and teat-seeking behaviour culminating in successful sucking bouts. Thus, lamb survival could be viewed as a successful 'partnership' between ewe and lamb behaviours until weaning (EVERETT-HINCKS *et al.* 2005). Neonates with difficult births have greater odds of having poor vigour (RILEY *et al.* 2004). Neonatal vigour is an important indicator of survival in many species (in pigs, BAXTER *et al.* 2008; in zebu cattle, DA

COSTA *et al.* 2008) and has knock-on consequences on the latency for neonates to suck successfully (TUCHSCHERER *et al.* 2000; HERPIN *et al.* 2002; DWYER 2003; DWYER *et al.* 2003; BAXTER *et al.* 2008). Thus, it seems appropriate to study lamb vigour and to determine how lamb behaviour influences later development.

1.2 Definition of lamb vigour

For the purposes of this thesis, lamb vigour is defined as the rate of progression of neonatal behaviours immediately after birth, i.e. the lamb is born, learns to stand and seek out the udder, culminating in a successful sucking bout. These behaviours show progress of conscious muscular control. A low vigour lamb will take longer to complete this behavioural progression than a lamb with higher vigour.

1.3 Consequences of poor lamb vigour

Rate of progression of behaviours has been linked to lamb survival (DWYER *et al.* 2001), where lambs which were slow to stand had reduced survival to 8 weeks of age. Low vigour lambs are slow to find the udder and display delayed sucking reflexes, and such slow behavioural progression may have several consequences for the lamb: lambs slow to stand and suck are at risk of depleting their energy reserves (Nowak and Poindron 2006), being unable to maintain homeothermy (ALEXANDER and WILLIAMS 1968), and risk developing hypothermia (GROMMERS *et al.* 1985; DWYER and MORGAN 2006; POLLARD 2006). There is also the risk of reduced absorption of immunoglobulins (Nowak and Poindron 2006) and impaired mother-young bonding (NOWAK *et al.* 1997; DWYER *et al.* 2003; NOWAK *et al.* 2007), which may result in poor maternal care and early lamb death (NOWAK 1996). The consequences of reduced intake of colostrum and mismothering are discussed below.

The colostrum produced at the time of birth, and for a few hours after, provides the lamb with nutriment and antibodies (PFEFFER *et al.* 2005). Newborn lambs are immunologically naïve at birth since immunoglobulins do not pass over the ovine placenta (BRAMBELL 1970; CHUCRI *et al.* 2010). This results in newborn lambs being vulnerable to infectious disease until sufficient colostrum has been ingested to provide passive immunity (NOWAK and POINDRON 2006). This may place lambs which are slow to suck at a disadvantage; both due to the lack of passive immunity and because energy intake is reduced, resulting in a greater loss of energy reserves (SAWYER *et al.* 1977; NOWAK and POINDRON 2006). Lambs acquire immunoglobulins via passage through the intestinal wall, however, the gut wall ceases to absorb large molecules by 6-8 hours after birth (AL-JAWAD and LEES 1985). Therefore, delays in suckling, due to either slowness to suck or inadequate maternal care, or an insufficient uptake of immunoglobulin, risks impairing the developing immune system (SAWYER *et al.* 1977), leading to an increased risk of mortality due to infections (NOWAK and POINDRON 2006). Once the lamb is sucking successfully, serum immunoglobulins rise rapidly during the first hour of ingestion and peak at 24 hours after birth (EALES and SMALL 1981). Interestingly, colostrum also acts to speed up the process of gut closure (VUKAVIC 1984), thus reducing the opportunity for other macromolecules from entering the lamb via the gut and, therefore, reducing the risks of infection (CAMPBELL *et al.* 1977).

Lambs with poor sucking ability may also have impaired mother-young bonding. Development of mother preference is mostly dependent on the first successful sucking bouts (NOWAK *et al.* 1997; NOWAK and POINDRON 2006) and is the earliest indicator of postnatal learning (VINCE 1993; VAL-LAILLET *et al.* 2009). The inability to suck during the first few hours after birth reduces the ability of the lamb to discriminate its mother, an effect that cannot be attributed to reduced colostrum intake (NOWAK *et al.* 1997; VAL-LAILLET *et al.* 2004). A reduction in sucking events during early lactation, due to inadequate mother-young bonding, may also result in a drop-off in milk production in the ewe (MARNET and MCKUSICK 2000; CIMEN and KARAALP 2009).

Lamb vigour is important because if the lamb does not provide the correct stimulus, the ewe may not be provided with the correct feedback to spark maternal interest or behaviour. The ewe needs a combination of hormones and behavioural response from the lamb at the right time after birth (DWYER and LAWRENCE 1997) for recognition and bonding to occur. Neonatal lamb activity is largely independent of the ewe behaviour; however, sucking behaviour is modified by ewe behaviour which may affect the strength of the ewe-lamb bond (DWYER and LAWRENCE 1999). After parturition, maternal grooming dries, cleans and stimulates the lamb and helps the bonding between ewe and lamb (NOWAK and POINDRON 2006), although DWYER and LAWRENCE (1999) suggest that lamb behaviour has no effect on the initiation of the ewe bonding behaviours. Interestingly, single lambs have a stronger attraction to their mothers than twins (NOWAK *et al.* 1989), which may be attributed to the amount of time that the ewe experiences with a single lamb, whereas the ewe's attention is split between twins, resulting in the ewe spending less time grooming individual twins than singles (O'CONNOR *et al.* 1992).

1.4 Management interventions to reduce lamb mortality

1.4.1 Human assistance at parturition

In intensive systems, lamb mortality during parturition and the neonatal period is minimised through supervision and assistance (NAWAZ and MEYER 1992). However, while this reduces the incidence of stillbirth due to difficult births, the incidence of mortality (of both ewe and lamb) due to infection can increase (BINNS *et al.* 2002). Human intervention at birth requires a considerable investment of labour to ensure lamb survival (FISHER 2003), with the bulk of human input directed towards assisting difficult births and ensuring lambs suck quickly afterwards (DWYER and LAWRENCE 2005a). Dystocia has been reported to be one of the primary causes of mortality within the first 3 days after birth (KERSLAKE *et al.* 2005). In addition, the management system in use often dictates which type of lamb mortality is prevalent on farm; outdoor systems suffer higher mortality from starvation or exposure to the weather (FISHER and MELLOR 2002) and perhaps predation (HAUGHEY 1993), whereas indoor systems suffer higher mortality due to infection (BINNS *et al.* 2002), either from close proximity to other animals or introduced by poor hygiene of stock workers. For the ewe, the physical act of assistance at birth may lead to pain as a result of pressure applied to extract the lamb (SCOTT 2005). Pain at parturition has widespread physiological effects on both ewe and lamb, where pain promotes maternal acidosis and its development in the lamb (BROWNRIDGE 1995). Acidosis, when the pH of blood plasma falls below 7.35, has the potential to alter brain function due to hypoxia and may also cause weight loss, muscle weakness and bone pains (GREENBERG *et al.* 1966; HUBER 1976). In addition, foetal acidosis may potentially be caused by any added stress during parturition (SHNIDER *et al.* 1979).

Advocates of a natural state (i.e. as the animals would be prior to artificial selection for production traits) commonly state that the welfare of animals would be better if human interference had not occurred or was to cease (MELLOR and STAFFORD 2003). Mortality figures of unassisted newborn farm animals from 50 years ago suggest that figures of 30-50+% were common (MELLOR and STAFFORD 2004), however, increasing knowledge about human intervention may reduce these figures to 25% or less (MELLOR and STAFFORD 2003). While this intervention has reduced mortality rates to between 15-30% (NOWAK *et al.* 2000; SAWALHA *et al.* 2007; BRIEN *et al.* 2010) there still appears to be a considerable problem of lamb mortality, although, some systems of low-input birth management have been developed which also manage to reduce neonatal mortality (FISHER and MELLOR 2002).

Aside from the labour implications of human intervention at birth, there may be unintended behavioural consequences to human intervention during parturition. At the beginning of parturition, ewes isolate themselves from the rest of the flock (ALEXANDER *et al.* 1990a); however, high stocking density in the lambing sheds may prevent isolation-seeking behaviours from being displayed (GONYOU and STOOKEY 1985). As a consequence, the high stocking density and disturbance from other ewes and stockmen during the birth process may compromise ewe-lamb bonding, by drawing the lamb's attention away from the dam or removal of the dam from the birth-site (FISHER and MELLOR 2002; DWYER 2003), with the added possibility that the ewe may experience high levels of emotional stress (DWYER and BORNETT 2004) leading to poor maternal care, mis-mothering and early death of the lamb (GONYOU and STOOKEY 1985; NOWAK 1996; NOWAK *et al.* 2006). In addition to the literature published about the adverse effects of assistance at birth, anecdotal evidence suggests that some stockmen routinely feed newborn lambs with colostrum shortly after birth; while this may help prevent deaths due to slowness to suck, it may also impair the development of the mother-young bond by disrupting the teat-seeking behaviour of the young and therefore the stimulus for the ewe to display maternal behaviours.

Some breeds, especially terminal sire breeds such as the Suffolk or Texel, often receive a high level of assistance at lambing due to having difficulties at birth and having lambs which are slow to stand and suck (DWYER *et al.* 1996; DWYER and LAWRENCE 2005a). In addition, the intensification of sheep farming has seen the average flock size increase from 209 in 1983 to 550 in 2003 with no corresponding increase in skilled labour (SCOTT 2005). However, the sheep industry is currently going through a change in outlook; many of the traditional, labour intensive systems currently used are proving to be unprofitable and unsustainable in the long term economic climate. Therefore, the current trend is to move towards lower input management systems, where greater emphasis will be placed on the adaptation of animals to their environment and their behavioural characteristics to stressors (CONINGTON *et al.* 2010) .

1.4.2 Nutritional supplementation

It is possible that lamb survival may be improved by improving the nutrition of the ewe during pregnancy. Adequate ewe nutrition during pregnancy has important consequences for foetal development and lamb survival, affecting embryo development, foetal growth and neonatal vigour and survival (ROBINSON *et al.* 2002). Maternal undernutrition has been linked to lamb survival (BINNS *et al.* 2002; DWYER and BORNETT 2004) since ewes which are undernourished in pregnancy have been reported to give birth to light weight lambs (ROBINSON *et al.* 1999). However, evidence suggests that any effect of undernutrition in early pregnancy may be breed-dependant since a study looking at the effects of undernutrition between days 1-90 of pregnancy indicated that lambs from a hill breed showed no effects on birth weight whereas lambs from a lowland breed weighed less at birth (ROOKE *et al.* 2010). The subject of nutritional supplements has been reviewed by ROOKE *et al.* (2008) for the express purpose of improving lamb vigour, physiology and immune function and the suggestion was that the evidence pointed to the involvement of selenium, vitamin E and fatty acids in improvement of lamb survival.

Studies looking at the inclusion of selenium in ewe diet during pregnancy have returned positive results (MUNOZ *et al.* 2008), reporting that lambs from selenium-supplemented ewes had improved immune systems and displayed a faster progression to stand than lambs from control ewes, although, there was no corresponding increase in lamb survival. Similarly, studies looking at supplementing the ewe diet in late gestation with vitamin E found a significant increase in lamb vigour response between ewes which had no vitamin E in the diet and those supplemented with vitamin E (ROOKE *et al.* 2008). However, there was no additional benefit conferred in supplementing higher concentrations of vitamin E (ROOKE *et al.* 2009). A study looking at the effects of supplementation with fish oil found that neither lamb birth weight, colostrum intake nor the status of lambs was affected by the addition of fish oil into the ewe's diet during the final 6 weeks of pregnancy (ANNETT *et al.* 2009). This is in contrast with pig studies which suggest that fish oil supplementation in early life can benefit neonatal immune function (CARROLL *et al.* 2003), aid in the development of the central nervous system resulting in a reduced latency from birth to sucking (ROOKE *et al.* 2001a; ROOKE *et al.* 2001b), and lower the incidences of piglet mortality (CORDOBA *et al.* 2000).

1.5 Breeding for genetic improvement

Anecdotally, farmers put considerable effort into the technological and management approaches for improving neonatal survival. However, recent worldwide mortality data (15-30%; NOWAK *et al.* 2000; SAWALHA *et al.* 2007; BRIEN *et al.* 2010) suggest there is more that needs to be done to reduce lamb mortality. By exploring the ewe and lamb behaviours around parturition and after birth, it may be possible to present a successful genetic approach for improving neonatal survival. By dissecting the phenotypic variation present in these traits we can discover how much variation is due to genetic or to environmental factors, thus gauging the success of breeding methods to improve the situation.

Heritability is a measure of the fraction of the phenotype variability that can be attributed to (additive) genetic variation (FALCONER and MACKAY 1996).Thus, it could be said that the heritability of a trait is a measure of how much an offspring resembles its parents, ranging from 0 to 1.0 (0 denotes no resemblance, 1 denotes 100%). Heritability is a measure of the relationship between phenotype (performance) and genotype (breeding value) of an individual, and is estimated using individual performance records of that trait, coupled with those individuals' pedigrees, allowing the genetic relationship between animals to be established. An estimate of heritability applies to the considered trait, to the specific population and a given point in time; moreover, the heritability of a given trait may vary both within- and between- populations or breeds and also over time. In the context of this thesis it should be noted that trait specific heritabilities are strictly only comparable between studies if the trait has been quantified by the same method. Every method is associated with a certain measurement error, which affects the magnitude of the environmental variance. In other words, if a given method results in moderate or high heritabilities, this indicates that the accuracy of the method was sufficiently high, or as *argumentum e contrario* a low heritability can also be due to an inaccurate method of measurement and does not always indicate a low level of inheritance.

Traits which are highly heritable (> 0.40) indicate that the phenotype of an animal is a good indicator of its genetic merit. Traits with low heritability (< 0.15) suggest that the phenotype is less reliable as an indicator (CASSEL 2009). Genetic progress is a product of the intensity of selection multiplied by the heritability of the trait in question multiplied by the phenotypic standard deviation of that trait (FALCONER and MACKAY 1996); if any of these estimates is low, then genetic progress will be slow. Therefore, a trait with higher heritability will show faster genetic progress than a trait with a lower heritability. This does not imply that traits with lower heritabilities should not be considered suitable for selection purposes but selection response and genetic progress will be low and slow. As genetic improvement is cumulative, cost-effective and results in a permanent change genetic solutions are sustainable and provide benefits for future generations (SIMM 1998). It should be mentioned that taking repeated measurements can increase the accuracy of the measurement and thereby increase the heritability, which is especially noteworthy when considering traits with low heritabilities.

However, while some traits can be measured more than once, for instance weight gain and wool staple length, many of the fitness traits have only a single measurement opportunity, such as latency from birth to standing. It is important to estimate not only heritabilities for the traits of interest but also the genetic correlations to other production and welfare traits in order to ensure that antagonistic genetic relations can be detected and accounted for with in the breeding programme.

1.5.1 Maternal trait selection for reproductive traits

Lamb survival is a complex composite trait, which is influenced by many components including uterine and other maternal reproductive traits, parturition, newborn viability and the mothering ability of the ewe. The genetic effect of each component varies (SAFARI *et al.* 2005) while the phenotypic variation present in a composite trait is influenced by the level of variability among the component traits and their interactions (SNOWDER 2002). Since genetic and environmental factors interact, genetic improvement of reproduction, and subsequent lamb survival, is very complicated (SNOWDER 2008). It stands to reason that improvements in lamb mortality may be effected by selection of desirable ewe reproductive characteristics. For instance, lamb welfare may be improved via selection of ewes with the ability to wean the number of lambs to which she gives birth (CONINGTON *et al.* 2004). Interestingly, CLOETE and SCHOLTZ (1998) report that selection for number of lambs reared, over a 16 year period, resulted in greater vigour in lamb sucking behaviour, while CLOETE *et al*. (2005) report a significant increase in lamb survival to rearing, an improvement in maternal behaviour and stronger dam-offspring bonding.

Selection for litter size at birth (the number of lambs born) or number of lambs weaned has commonly been practised (SNOWDER 2008) since litter size is easy to record and heritabilities are generally higher than other reproductive traits such as lamb survival or fertility (RAO and NOTTER 2000). The number of lambs born in a litter has consequences for survival, with mortality increasing as litter size increases (CLOETE 1992; DWYER and LAWRENCE 1998). SAFARI *et al* (2005) and RAO and NOTTER (2000) report the heritability of the number of lambs born as a direct genetic effect of the ewe at approximately 0.10, whereas a study distinguishing between direct and maternal effects found little evidence of maternal genetic effect on number of lambs born nor on the number of lambs born alive, 0.01 and 0.01 respectively (ROSATI *et al.* 2002). Heritabilities for lamb survival, considered as a trait of the ewe, and ewe rearing-ability have been estimated at 0.03 and 0.06, respectively (SAFARI *et al.* 2005), suggesting that genetic progress in these traits would be possible but slow. However, selection for a single component of such a complex trait does not necessarily mean that there will be an overall improvement in that trait, and there may be a negative correlated response in another component of the trait (SNOWDER 2002).

In addition to selection based on quantitative reproductive traits, it may be possible to select for ewe behaviour traits such as maternal behaviour scores (O'CONNOR *et al.* 1985). Maternal behaviour scores are based on the proximity of the ewe during handling of the lamb, and have been reportedly related to postnatal lamb survival and weaning weight (O'CONNOR *et al.* 1985; LAMBE *et al.* 2001; EVERETT-HINCKS *et al.*

2005; SAWALHA *et al.* 2007). Additionally, it may be possible to select ewes upon the specific behaviours displayed around parturition. Behaviours such as licking and grooming, low-pitched bleating and cooperation with lamb sucking behaviours enhance ewe-lamb bonding and recognition (ALEXANDER 1988; NOWAK *et al.* 1997; DWYER 2008a). However, there are currently no reported heritabilities for these maternal behaviours available (CONINGTON *et al.* 2010).

In general, heritabilities for reproductive traits (for example, lamb survival 0.03 to 0.33 (SAWALHA *et al.* 2007; AFOLAYAN *et al.* 2008) and litter size, 0.19 (AFOLAYAN *et al.* 2008)) seem to be generally lower than those for performance traits (for example, average daily gain 0.14 to 0.30 (MAXA *et al.* 2007), carcass fat 0.20 to 0.37 (GREEFF *et al.* 2008) and wool 0.25 to 0.32 (BORG *et al.* 2009)). However, greater phenotypic variation appears to be present in reproductive traits than performance traits. Records of lambing performance over a period of time could provide indirect selection criteria for reproduction characteristics, and therefore heritabilities and Estimated Breeding Values for reproduction characteristics could be added to breeding programmes (AFOLAYAN *et al.* 2008).

1.5.2 Direct selection to reduce lamb mortality

As we have seen, there is the possibility that lamb mortality may be improved by management interventions and by selection for improved maternal care, and maternal selection may show improvement in a ewe’s mothering ability, but there is still the problem of lamb viability after birth. In general, terminal-sire sheep breeds are genetically selected for high lean growth and other carcass [or morphological] traits (AMER *et al.* 2007; BYRNE *et al.* 2010) and, in addition, on extremes of conformation and bone (RIUS-VILARRASA *et al.* 2010). A study by SMITH (1977) states that artificial selection for production traits, such as growth rate and mature size, may be carried out with no consideration required for dystocia and lamb vigour, due to their low heritabilities, 0.13 and 0.10, respectively. However, BOMAN (2011) warns that selection for specific traits may constitute an unpredictable risk of unwanted side-effects and a subsequent risk of substantial loss of genetic variation in other traits, i.e. selection for increased muscle mass and bone structure may have resulted in an increase in dystocia at birth in terminal sire breeds (GROMMERS *et al.* 1985; DWYER and BUNGER in press).

Genetic solutions to reduce lamb mortality and its main causes (dystocia and low vigour lambs) are desirable. There are at least two possible solutions available: (i) the use of suitable breeds or strains to cross into existing flocks, and (ii) intrabreed selection, where selection within flock or breeds occurs. Approach (i) requires the existence of breed/strain differences in the desired traits. Care must be taken when selecting suitable breed/strain candidates, however. If the ultimate aim of a breeding programme is to produce lambs with superior carcass qualities (such as terminal sire breeds), choosing a hill-breed cross would not be desirable. Approach (ii) needs sufficient intrabreed genetic variance in specific traits for selection to be successful. Producers of breeds which have low genetic variance in a desirable trait will find progress too slow to be a practical tool for selection. Conversely, breeds with high genetic variance will show faster progress in a given trait depending on the breeding objectives.

Another option to reduce lamb mortality would be to directly select for improved neonatal behaviour and welfare traits, such as the ability for a lamb to be born easily and the ability to stand and suck quickly. This would entail selecting individual animals with superior neonatal traits at birth and using them in breeding programmes. So, only animals which themselves had an easy birth, stood quickly and sucked quickly would pass on their genotype to the subsequent generations. Of course, since selection is carried out on phenotypes rather than genotypes, therefore there would need to be reliable and consistent methods for measuring neonatal traits.

1.6 How can neonatal behaviour traits be quantified?

Several different scoring systems have been used to record levels of dystocia/birth assistance. Most dystocia scoring systems refer to the amount of human assistance given. SPEAR-SMITH *et al.,* (2000) uses a categorical 5-point scale which specified the area where the lamb is pulled from, i.e. birth canal or uterus. This system requires trained observers and is very labour intensive. This type of research-focussed approach does not lend itself to being useful on farm, where stockmen are not trained in anatomy and are under time constraints. Other systems use scales ranging from 1-4; where a score of 1 represents no assistance given, a score of 2 represents slight assistance, a score of 3 represents a difficult birth with manual delivery and a score of 4 represents a difficult delivery or vet assistance (SPEIJERS *et al.* 2010).

Methods for measuring lamb vigour vary greatly between studies. Several studies have used time-based values, i.e. the latency between birth and standing or appearing to suck (ALEXANDER *et al.* 1990b; DWYER 2003; BRIEN *et al.* 2009). However, timed behaviour traits are not easy and quick to measure for on-farm when compared to categorical indicator traits (BRIEN *et al.* 2009). Spear-Smith *et al.,* (2000) have used a vigour score based upon the Apgar score for newborn human infants measured at 1 hour after birth. This 5-point scale ranges from 1, dead; 2, can not stand; 3, minimal vigour; 4, moderate vigour; and, 5, very vigorous. While this score was based upon a lamb's ability to stand, nurse or walk, the score descriptions are vague and subjective for scores 3-5, while the time-scale is not practical for on-farm data collection.

Studies have reported breed differences in the latency from birth to standing for 10 seconds (SLEE and SPRINGBETT 1986) and line differences in the latency from standing to sucking, suggesting that variation in the rate at which a lamb stands and sucks may be partially genetic (CLOETE and SCHOLTZ 1998; see also DWYER *et al.* 2001 for sire effects). Therefore, since line and breed differences are found, and selection for lamb survival has been successful (KNIGHT *et al.* 1988; KILGOUR and HAUGHEY 1993; CLOETE and SCHOLTZ 1998), it would suggest that there is a genetic basis to lambing difficulty and lamb vigour (ALEXANDER *et al.* 1990c; CLOETE and SCHOLTZ 1998; CLOETE *et al.* 2002). However, genetic parameter estimates for behavioural traits contributing to lamb survival are scarce (HOHENBOKEN 1985; HINCH 1997; MACFARLANE *et al.* 2010b). Heritabilities for lamb vigour behaviours (for example, latency from birth to standing) appear low and range from 0.1 to 0.22, and latency from standing to sucking range from 0.08 to 0.12 (CLOETE *et al.* 2002)). So, not only would the genetic progress on these traits (latency to stand and latency to suck) be slow, the collection of these measurements would be time-consuming and costly to implement in an on-farm basis.

Behaviour traits are often difficult or time-consuming to measure and, as a result studies generally have fewer animals. Indeed, in an overview of behavioural genetics, FAURE (1994) suggests that the subject of behavioural genetics is rarely studied because most behaviour is perceived as being mainly environmentally determined and that behaviour is perceived to be difficult to measure. A meta-analysis by MOUSSEAU and ROFF (1987) suggests that there were four categories of traits used in genetic studies: (i) behavioural, e.g. activity, conditioning sensitivity, alarm reactivity; (ii) life history, e.g. fecundity, viability, survival; (iii) morphological, e.g. body size and other metric characters (such as production traits); and, (iv) physiological, e.g. oxygen consumption, body temperature, resistance to heat stress. Of all these categories, the traits easiest to quantify are the morphological and physiological traits; life history and behavioural traits are frequently qualitative and are often ephemeral in nature.

As a consequence, reproductive and behavioural traits, especially those related to development are difficult to quantify on farm – a considerable inconvenience considering the large amounts of data needed. Thus, it follows that proxy methods of measurement (scoring systems) are needed to measure such qualitative traits in a manner that allows for collection of sufficient volume of data to enable genetic analysis. Scoring systems need to be easy-to-use to allow them to be incorporated into on-farm breeding programmes and are more likely to be adopted if they integrate well with the management routine already in place. Such scoring systems also need to be objective, biologically meaningful, repeatable and reflective of what is happening behaviourally. Once such scoring systems are developed, the traits measured need to be recorded in large data sets with the intention of estimating heritabilities, and thus determining the suitability of these traits for selection purposes. As outlined above, a proxy method has the potential to reduce the true heritability of a trait, but on the other hand, it increases accuracy of the heritability estimates as it can be applied to larger numbers of animal. In addition, if a moderate or high heritability has been found it may indicate that the method reflects at least a reasonable part of the genetic variance.

1.7 Thesis aims

The overall aim of this thesis was to investigate whether it is possible to reduce the amount of human intervention at lambing through genetic methods. There are at least two possible genetic solutions available to achieve this: (i) introgression of genes from suitable breeds or strains and (ii) intrabreed selection. Approach (i) requires the existence of breed/strain differences in the desired traits and approach (ii) needs sufficient intrabreed genetic variance. Thus, there needs to be suitable methods for quantifying neonatal lamb behaviour in an ‘on farm’ environment, which are suitable for estimating the heritability of neonatal behaviours. This would allow the investigation of whether it is possible to improve the welfare of lambs through selection of parents with superior vigour and lambing ease characteristics.

The specific aims of this thesis were:

- To provide suitable scoring methods for measuring neonatal behaviour and welfare traits on farm.
- Examine possible differences in neonatal behaviour using the scoring methods developed between the three main Suffolk strains currently in use as sires in the UK.
- To determine whether the neonatal behaviour traits are heritable, and to estimate the phenotypic and genetic correlations between the traits, using a sub-population of Texel lambs from an SAC Research farm.
- To test the feasibility of neonatal data collection ‘on farm’ with the Industrial Partner, the Suffolk Sheep Society (UK).
- To estimate genetic variance and heritabilities for the neonatal behaviour traits, and to determine the relationship between the neonatal traits and between neonatal and later production traits.

Thus, Approach (i) was investigated in chapter three, with the results considered unsatisfactory. Approach (ii) was tested in chapters four and five, with the results indicating that this approach is both feasible and effective.

1.8 Thesis outline

This thesis is divided into 6 further chapters.

Chapter two describes the development of scoring systems for quantifying neonatal lamb fitness and behaviour traits. Detailed historical behaviour data were analysed to develop criteria for three scores: birth assistance, lamb vigour and sucking assistance. These scoring systems were then validated in a separate flock by simultaneously recording scores and the latency to perform certain landmark behaviours.

In chapter three, the theory of introgressing genes from a strain selected for superior lambing and neonatal behaviour was tested. Neonatal scores from cross-bred lambs sired by rams from each of the three main Suffolk strains currently used in the UK were compared to determine whether the three strains differed in their neonatal characteristics.

In **chapter four**, neonatal scores were recorded in an experimental flock of pure-bred Texel sheep for the purpose of estimating genetics parameters for each trait. This chapter advances the suggestion that selection for neonatal behaviour traits using the proxy method developed in chapter two is both feasible and effective.

In **chapter five**, neonatal scores from an industry-generated database were analysed to report the genetic variance present within pure-bred Suffolk sheep belonging to members of the industrial partner, the Suffolk Sheep Society (UK). This chapter assesses the feasibility of recording neonatal traits 'on farm' and the relationship between neonatal traits and production traits. This chapter also introduces the theory that neonatal traits influence farmer breeding and recording decisions.

Chapter six describes a pilot study which investigates whether neonatal lamb traits relate to faecal soiling at weaning. The relationships between neonatal scores and weaning weight, growth rate and degree of faecal soiling (dag score) of lambs from 3 breeds (Scottish Blackface, Texel and Suffolk) were assessed.

Finally, a general discussion in **chapter seven** combines the findings of the experimental chapters into overall conclusions. There is no separate literature review, as chapters are written in the style of scientific papers and each contains a review and associated bibliography of the relevant literature for that chapter.

In addition,

Appendix I is the basic analysis of the neonatal scores from Chapter 3 (Lambing ease and lamb vigour characteristics in lambs sired by rams of three Suffolk strains) with the removal of the covariate of birth weight and the fixed effects of the neonatal scores.

Appendix II is the basic analysis of the neonatal scores from Chapter 4 (Genetic parameters for birth assistance in a pure-bred Texel population accounting for Texel double muscling QTL (TM-QTL) genotypes) with the removal of the covariate of birth weight and the fixed effects of the neonatal scores.

Appendix III is the basic analysis of the neonatal scores from Chapter 5 (Genetic parameters for fitness and neonatal behaviour traits in Suffolk sheep) with the removal of the covariate of birth weight and the fixed effects of the neonatal scores.

These appendices allow the comparison of the fixed effects in a practical versus biological sense (the main chapters show the differences from a biological stand-point).

<u>Note</u>: For the mixed model analysis, least square mean values are estimated marginal means over a balanced population. The matrix used to compute the means is the same as the matrix formed in a GLM model; however, the standard errors are adjusted for the covariance parameters in the mixed model. This results in higher standard errors than found in a GLM.

CHAPTER TWO

DEVELOPMENT AND VALIDATION OF ON-FARM BEHAVIOURAL SCORING SYSTEMS TO ASSESS BIRTH ASSISTANCE AND LAMB VIGOUR

Published in Animal: 5(5): 776-783

2.1 Abstract

Lamb mortality remains a significant welfare and economic issue for sheep production. Lamb survival is to a degree dependent upon an easy delivery and the expression of appropriate behaviours from both mother and offspring, such as rapid standing, udder-seeking and sucking by the lamb. Genetic solutions have the potential to improve birth assistance and lamb behaviour but large amounts of data are needed. Therefore, to achieve this objective, simple, proxy methods (scoring systems) were developed to quantify the level of birth difficulties and lamb vigour on farm. In the first study, detailed historical behavioural data from 1,156 lambs (Scottish Blackface and Suffolk) were analysed to develop criteria for 3 scores: birth assistance, lamb vigour, and sucking assistance.

The birth assistance score was developed by analysing the relationships between birth presentation and intervention levels, and intervention level and labour length. Lambs with abnormal birth positions required more assistance than normally presented lambs and lambs with long parturitions required more and greater assistance than those with short parturitions. Lamb vigour score was developed by analysing the latencies for the lamb to first perform specific behaviours; more vigorous lambs reach landmark behaviours faster than low vigour lambs. The sucking assistance score was developed from the relationship between the latency to suck successfully and assistance level, where lambs which were slow to suck required more assistance than lambs that were quick to suck.

In the second study, the behaviour scoring systems (5-point categorical scales) were validated using a commercial flock of 80 twin-bearing cross-bred ewes mated with either Texel or Suffolk sires by simultaneously recording scores and the latency to perform specific landmark behaviours (i.e. to stand, seek the udder and suck). The vigour scores (recorded at 5 min of age) were compared with the latency from birth to standing and showed that lambs with lower (better) vigour scores were faster to stand after birth than those with higher scores. The sucking assistance scores were compared with the latency from birth to sucking, and showed that lambs with lower

sucking assistance scores are quicker to suck than those with high scores. These results demonstrated that the scoring systems could provide a practical and reliable assessment of birth assistance and lamb behaviour on farm and were sufficiently sensitive to discriminate vigour levels between lambs sired by either Suffolk or Texel rams.

2.2 Implications

Scoring systems have been developed for use, on farm, to assess simply and rapidly birth difficulty, lamb vigour and sucking assistance, traits which are important for the survival of newborn and neonatal lambs. These scores provide a means of readily assessing important behavioural traits, which are time-consuming to record, on farm. These neonatal lamb scoring systems have potential for use in selection of animals with greater genetic merit for low birth assistance and improved neonatal vigour traits. The systems may also be of use in management decisions and for animal welfare assessment.

2.3 Introduction

Lamb mortality remains a significant welfare and production issue for the sheep industry. Mortality rates are highest within the first 3 days of postnatal life (NOWAK *et al.* 2000; SAWALHA *et al.* 2007), as a consequence of complex interactions between difficult births, low lamb vigour, poor maternal care, infection and starvation/hypothermia. In intensive systems, lamb mortality during parturition and the neonatal period is minimised through supervision and assistance. However, while the incidence of stillbirths due to dystocia is decreased, mortality (of both ewe and lamb) due to infections can increase (BINNS *et al.* 2002). High stocking density within the lambing shed can also compromise ewe-lamb bonding: the isolation-seeking behaviour of the parturient ewe may be disrupted, resulting in an increase in stress and the possibility of a prolonged labour (POINDRON *et al.* 1997) thus increasing the incidence of mis-mothering (GONYOU and STOOKEY 1985).

Human intervention at birth requires a considerable investment of labour to ensure lamb survival (FISHER 2003), and substantial human input is directed towards assisting difficult parturitions and ensuring that lambs suck quickly thereafter (DWYER and LAWRENCE 2005a). As farm incomes and subsidy payments decrease, low input management systems are becoming more common as farmers attempt to reduce labour costs and as a consequence increase the number of sheep per stockperson. Therefore, to achieve a lower input system, without impacting upon welfare, lambs need to be delivered easily, be active, vigorous and able to suck from their mothers unaided (DWYER and LAWRENCE 2005a). Improvements in ease of delivery and lamb vigour are therefore important not only to reduce labour input at lambing, but also to improve lamb survival and welfare (DWYER 2008b). These traits can be improved by management interventions, and can also potentially be addressed by genetic selection, which results in permanent and cumulative response and has the potential to reduce labour costs.

Heritabilities for reproductive traits (for example, lamb survival 0.03 to 0.33 (SAWALHA *et al.* 2007; AFOLAYAN *et al.* 2008) and litter size, 0.19 (AFOLAYAN *et al.* 2008)) seem to be generally lower than those for performance traits (for example, average daily gain 0.14 to 0.30 (MAXA *et al.* 2007), carcass fat 0.20 to 0.37 (GREEFF *et al.* 2008) and wool 0.25 to 0.32 (BORG *et al.* 2009)). Heritabilities for lamb vigour behaviours (for example, latency from birth to standing) appear lower and range from 0.1 to 0.22, and latency from standing to sucking range from 0.08 to 0.12 (CLOETE *et al.* 2002)). However, greater phenotypic variation appears to be present in reproductive traits than performance traits (SAFARI *et al.* 2005) possibly due to a history of intensive selection for increasing performance traits coupled with little or no direct selection pressure on the behaviours related to reproduction. Records of lambing performance over a period of time could provide indirect selection criteria for reproductive characteristics, and therefore heritabilities and Estimated Breeding Values for reproductive characteristics could be added to breeding programmes (AFOLAYAN *et al.* 2008).

Reproductive and behavioural traits related to development are, however, difficult to quantify and measure on farm. Proxy methods of measurement (scoring systems) are needed to measure such qualitative traits in a manner that allows for collection of sufficient data to enable genetic analysis. Scoring systems need to be easy-to-use to allow them to be incorporated into on-farm breeding programmes and are more likely to be adopted if they integrate well with the management routine already in place. Such scoring systems also need to be objective, biologically meaningful, repeatable and reflective of what is happening behaviourally.

Therefore, the objectives of this study were to develop and validate scoring systems for birth assistance and neonatal lamb behaviour that could be easily implemented on farm and are correlated to underlying behavioural traits. In the first study, historical behavioural data were used to create scoring systems. The data, from more than 1100 lambs from two pure-breeds, Scottish Blackface and Suffolk, known to differ in lamb vigour (DWYER *et al.* 1996; DWYER and LAWRENCE 2005b; DWYER 2008a), were analysed as one group to assess the distribution of data across time. As expected, analysis of this data shows that each breed had a unique distribution within each scoring system. In the second study, score data and behavioural latency data were collected simultaneously using cross-bred ewes managed under commercial husbandry/housing conditions. The cross-bred ewes were mated with either Texel or Suffolk rams to test whether the scores were sensitive enough to discriminate between two of the lamb genotypes commonly produced in commercial flocks.

2.4 Materials and Methods

3.2.1 Study 1: Development of the Scoring Systems

3.2.1.1 Animals

Data from 1156 lambs were used to develop scoring systems classifying (1) birth assistance, (2) neonatal lamb vigour and (3) neonatal sucking ability. This data set contained information on length of labour, lamb presentation at birth and neonatal lamb behavioural latencies (see Table 2.1 for definition of lamb behaviour (DWYER *et al.* 1996)) collected from Scottish Blackface (SB) and Suffolk (S) flocks during the 2001-2005 and 2007 lambing seasons. For the purposes of developing the scores, data from both breeds were combined. These two breeds have been found to be divergent in behaviour (DWYER *et al.* 1996; DWYER and LAWRENCE 2005b) and, therefore the combination of SB and S were considered to sufficiently represent the variation within these traits that exist within the wider sheep population.

All ewes were allowed to give birth unaided, as far as possible, according to a standard lambing protocol. The protocol permitted assistance if the birth process failed to progress, i.e. if no lamb parts were seen 1 h after the appearance of fluids and/or 2 h after lamb parts had been seen with no other obvious progress. Any intervention was kept to a minimum, correcting presentational difficulties where possible before allowing the ewe to continue unaided. Certain specific presentations (breech, head back and two lambs together) required immediate assistance. The lamb, once born, was allowed 2 h to stand and successfully suck unaided. Any lambs which had not sucked by 2 h after birth were assisted. Behavioural data were collected on videotape and analysed by Observer 5.0 data recording software (NOLDUS *et al.* 2000) as previously described (DWYER 2003).

Three scoring systems were developed. The birth assistance score, a system based on the interaction between maternal effort and lamb presentation, consisted of data from 818 lambs for lamb presentation and 923 lambs for intervention levels and labour latencies. The lamb vigour score, based solely on the attributes of the lamb, consisted of data from 970 lambs for latency to first perform specific landmark behaviours (Table 2.1). Finally, the sucking assistance score, a score based on the interaction between lamb vigour and maternal behaviour, consisted of data from 964 lambs for the latency to suck successfully (Table 2.1) and amount of intervention required.

2.4.1.1 Statistics

Since the data were not normally distributed, all data were analysed using non-parametric tests in Minitab, version 15.1.20.0 (2007). Latency data were analysed using Kruskal-Wallis one-way-ANOVA.

Table 2.1. Ethogram of neonatal lamb behavioural progression. Latencies are measured as the time from birth to when specific behaviours are first displayed for the whole dataset.

Behaviour	Definition	n	Median Latency (seconds)	Interquartile range
Shake Head	Lamb lifts its head off the ground and shakes its head from side to side	971	42	23-77
Kneel	Lamb is lying on its chest, and pushes its chest off the ground supporting some of its weight on the knees	979	215	139-365
Attempt to Stand	Lamb supports weight on one or more hind legs while balanced on the knees of the front legs, duration must last for 5 seconds	958	409	283-706
Stand	Lamb supports it weight on all four legs, duration must last for 5 seconds	961	1023	675-1528
		Total n in whole dataset	**Median Latency (seconds)**	**Interquartile range**
Seek the Udder	Lamb must actively move towards the udder area and have its nose/mouth within 10 cm of the ewe's teat area	969	1257	909-2648
Unsuccessful Suck	Lamb has hold of the teat but either lets go of the teat or the ewe moves away causing the lamb to let go, lamb will usually be moving	933	2171	1282-3994
Successful Suck	Lamb latches onto teat, lamb may make sucking noises and/or waggle its tail, lamb will usually stand still	1021	5385	3286-10000

2.4.2 *Study 2: Validation of the Scoring Systems*

2.4.2.1 Animals

Validation of the birth assistance score was not required since it was based upon actual shepherd practices at lambing. The behavioural scoring systems (neonatal lamb vigour and neonatal sucking ability) were validated by collecting data at birth from 80 twin-bearing, 2-year old Scottish Blackface x Border Leicester ewes. The ewes had either been mated with Suffolk (n=42) or Texel rams (n=38). Ewes were group housed in straw pens (4.3m x 9.2m), in 4 groups of 20 ewes, approximately 9 weeks prior to lambing in order to accustom the ewes to the presence of observers. Hay and fresh drinking water were available *ad libitum* and 6 weeks prior to lambing ewes were fed a concentrate mix (g/kg; barley, 600; soya-bean meal, 200; molassed sugar beet pulp, 150; rapeseed meal 50) adjusted every two weeks in order to meet energy requirements for the advancing stages of pregnancy (AFRC 1993).

Observers were present for 24 h a day during lambing. Ewes were marked to allow identification from a distance. Ewes were assisted at birth according to the protocol described for study 1. After parturition the ewes and lambs were left undisturbed for 2 h. Scores for birth assistance, lamb vigour at 5 min of age and sucking assistance (Table 2.3) were collected for each lamb along with more detailed behavioural latency data (Table 2.1). Latency data were collected by recording the time of birth (using a stopwatch) and the time at which a specific behaviour occurred. Two h after the birth of the second lamb (or after the second lamb had sucked successfully, whichever happened first), the ewe and lambs were moved into individual straw-bedded pens (1.2m x 1.2m). Assuming no complications ewes and lambs stayed in the individual pens until 3 days after lambing, when they were turned out to pasture. *Ad libitum* hay and clean fresh drinking water were available in the individual pens. Ewes were fed concentrate mix to meet energy requirements.

2.4.2.2 Statistics

One ewe delivered two stillborn lambs; therefore 158 lambs provided data that were used in the validation. Since the data were not normally distributed, all data were analysed using non-parametric tests in Minitab, version 15.1.20.0 (2007). Latency data were analysed using Kruskal-Wallis one-way-ANOVA. Breed differences were investigated using Mann-Whitney U-tests with score proportions investigated using χ^2 tests.

2.5 Results and Discussion

2.5.1 Study 1: Development of the Scoring Systems

2.5.1.1 Birth Assistance

The birth assistance score was developed by considering the relationship between parturition length, lamb presentation and human intervention levels during parturition. Lambs that required no assistance (n=679) had a median labour length of 33.0 min (confidence intervals; 31.0-36.0 min). Therefore 30 min was selected as a practical cut-off point to divide lambs that required no assistance into two categories: no assistance with a labour of short duration (<30 min) and no assistance with a labour of long duration (>30 minutes; Figure 2.1). The no assistance class contained a group of animals that had other than normal presentation which were, nonetheless, able to give birth unaided (Table 2.2).

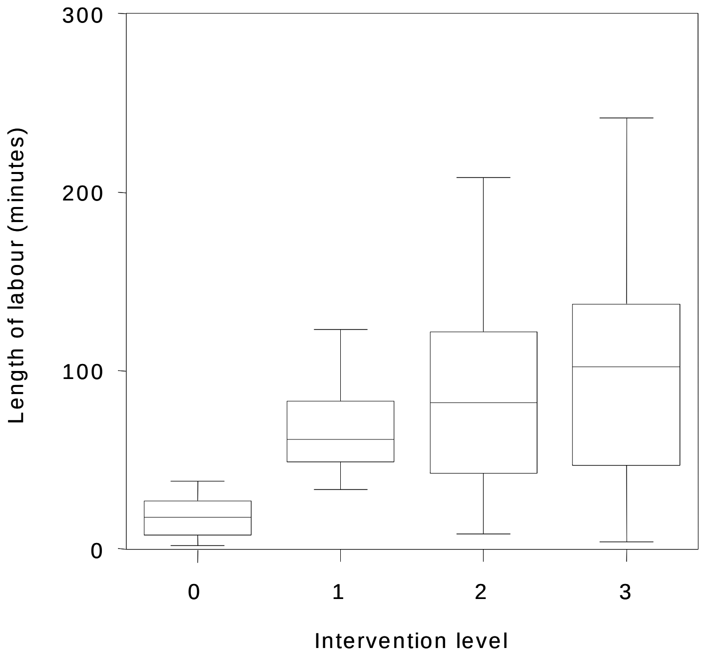


Figure 2.1. Relationship between length of labour and the need for different levels of intervention.

Table 2.2. Different presentations of Scottish Blackface and Suffolk lambs at birth. The total number of lambs within each presentation class and the proportions of that presentation within each assistance level are given. Note that there is no information about caesarean sections, which was classed separately as veterinary intervention.

Presentation	**Total n**	**No assistance – quick**	**No assistance – long**	**Minor assistance**	**Major assistance**
Normal	679	0.51	0.43	0.03	0.03
One leg back	53	0.21	0.32	0.30	0.17
Two legs back	41	0.02	0.07	0.59	0.32
Back legs first	11	0.27	0.18	0.18	0.36
Breech	19	0.21	0.16	0.16	0.47
Two lambs together	8	0.13	0.25	0.13	0.50
Head back	7	0.00	0.00	0.14	0.86

Data for assisted presentations were recorded as requiring either minor assistance (presentational difficulties which were corrected before the ewe was able to continue unaided; n=94), major assistance required (n= 45) or veterinary assistance (n=3). Table 2.2 shows that these categories reflected increasing deviation from a normal presentation: the minor assistance group mostly comprised of lambs presenting head first with either one or both legs back while major assistance comprised lambs presenting with head back, backwards, breech or multiple lambs together. Veterinary assistance comprised presentations too complicated for standard assistance. Each of the above categories was assigned a score value, with the best score given a value of 0 and the worst 4 (Table 2.3a). Length of labour increased significantly for each increase in intervention level/ score (Fig 2.1, $P<0.001$; note that there were no labour duration data available for veterinary intervention).

Table 2.3. Definitions of birth assistance scores, lamb vigour scores and sucking assistance scores.

Score	Description
(a)	**Birth assistance scores**
0	Unassisted or easy uncomplicated delivery of short duration (<30 min)
1	Unassisted or easy uncomplicated delivery of long duration (>30 min)
2	Minor assistance required. Presentation corrected, little effort needed to deliver lamb
3	Major assistance required. Difficult delivery needing effort to deliver lamb
4	Veterinary assistance required
(b)	**Lamb vigour scores**
0	Extremely active and vigorous lamb, has been standing on all 4 feet
1	Very active and vigorous lamb, standing on back legs and on knees
2	Active and vigorous lamb, on chest and holding head up
3	Weak lamb, lying flat, able to hold head up
4	Very weak lamb, unable to lift head, little movement
(c)	**Sucking assistance scores**
0	Lamb sucking well without assistance within 1 h
1	Lamb sucking well without assistance within 2 h
2	Lamb given sucking assistance/ fed by stomach tube once or twice in first 24 hours after birth
3	Lamb given sucking assistance, fed by stomach tube more than twice, needing help after 1 day old, but able to suck by 3 days old
4	Lamb still needing help to suck when more than 3 days old

Comparison of calculated birth assistance scores for S (n=424) and SB (n=525) lambs indicated that S lambs required a higher level of birth assistance than SB lambs (Table 2.4; χ^2 test, *P*=0.037).

Table 2.4. Qualifying criteria for each of the scoring systems (birth assistance, lamb vigour and sucking assistance) with the proportion (number) of Suffolk and Scottish Blackface lambs attaining that score. Note that no data were available for how much sucking assistance was required for those lambs that did not suck within 2.5 hours (marked as *).

Scoring system	Breed	Score									
		0		1		2		3		4	
Birth assistance	S	0.25	(105)	0.42	(180)	0.16	(66)	0.17	(73)	0	(0)
	SB	0.41	(209)	0.38	(195)	0.11	(55)	0.10	(51)	0.01	(3)
Lamb vigour	S	0.00	(0)	0.23	(107)	0.44	(205)	0.32	(149)	0.02	(8)
	SB	0.05	(28)	0.48	(286)	0.30	(107)	0.16	(94)	0.02	(11)
Sucking assistance	S	0.17	(72)	0.28	(117)	0.55*	(234*)	-	-	-	-
	SB	0.43	(231)	0.36	(192)	0.22*	(117*)	-	-	-	-

In general, as the length of parturition increased then more assistance was required (Fig 2.1). However, some of the more abnormal presentations were detected more quickly than others, as evidenced by Fig 2.1 where the minor and major assistance were associated with a wider range of labour lengths. Prolonged labours can increase the likelihood of lamb mortality and ewe rejection of the lamb (ALEXANDER *et al.* 1988; HAUGHEY 1993). In addition, human intervention during parturition is a considerable investment in labour and time (FISHER 2003) and reflects a high input system. Selection to reduce lambing difficulty could reduce human labour requirements and bring additional welfare benefits to ewe and lamb

2.5.1.2 Lamb Vigour

The lamb vigour score was developed by considering the range of behaviours displayed (Table 2.1) at a range of times after birth (2, 5, 10, 15 and 20 minutes), to identify a time which would give most information about lamb vigour but also be compatible with on-farm practice. Figure 2.2 shows the number of animals which had displayed a specific behaviour by the various time points. By 2 minutes of age, most of the lambs had shaken their heads but few had progressed to attempting to stand. For the later time points (10, 15 and 20 minutes), the majority of lambs had progressed to attempt to stand which left little variation available for distinguishing between individuals. The most even distribution of lambs into the different behaviours was given at 5 minutes after birth. Five minutes is useful as a length of time which keeps disruption of the management routine to a minimum. Therefore, the measurement of lamb vigour at 5 minutes post-delivery integrates well with intensive management systems. It is important to note that if the birth of the lamb is not observed then no score can be given to the lamb.

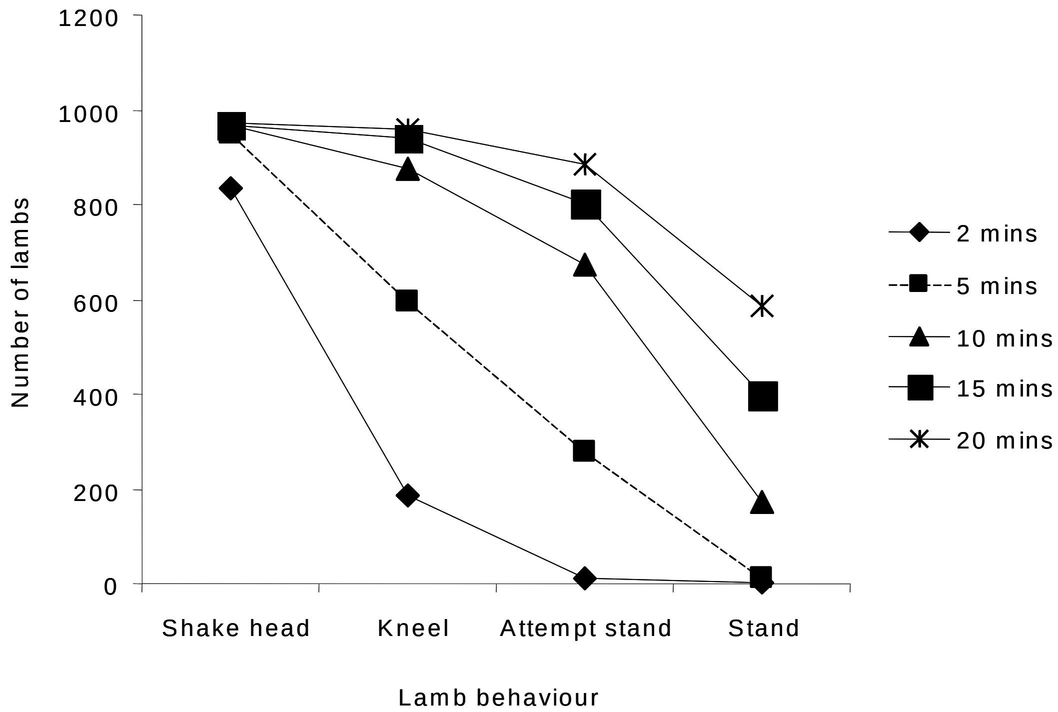


Figure 2.2. Number of lambs reaching specific landmark behaviours by certain time points after birth.

The behaviour of each lamb was analysed 5 min after birth thus creating the categories and scores shown in Table 2.3b. At 5 min after birth, lambs were either: standing (n=10), attempting to stand (n=264), kneeling (n=382), had head erect and self supported (n=300) or were unable to lift the head from the ground (n=26). A comparison of assigned scores for S (n=469) and SB (n=596) lambs indicated that S lambs had inferior vigour scores to SB lambs, (medians (with interquartile ranges): S=2 (2.00-2.00), SB=1 (1.00-2.00), P<0.001; Table 2.4).

2.5.1.2 Sucking Assistance

The sucking assistance score was developed by considering the relationship between latency to the first successful sucking event and the amount of human assistance required to keep the lamb alive. Lambs that required no assistance to suck (n=615) had a median time to suck successfully of 60 min (confidence intervals; 58.0-64.12 min). Therefore, lambs requiring no assistance were divided into two categories: sucked independently within one hour (n=309; median time to suck (interquartile range), 42.0 min (29.1-52.8)) and sucked independently between 1 hour and 2 hours after birth (n=306; median time to suck, 86.7 min (74.0-105.3)). Any lambs which had not sucked within 2 h were assisted (n=406). In order to quantify the amount of assistance required, the assisted category was split into: lamb given sucking assistance once or twice within 24 h; lamb given sucking assistance more than twice, needing help after 1 day old, but able to suck by 3 days of age; and, lamb still needing help to suck when more than 3 days old, i.e. assistance such as bottle-feeding a lamb which had a weak sucking-reflex or feeding a lamb too weak to suck by stomach tube. Each category was assigned a score value, with 0 for the best score (no assistance) and 4 for the worst (most assistance required), as shown in Table 2.3c. Note that there are no data available for the amount of sucking assistance given. The time points of 1 and 3 days were based upon practical experience and used to distinguish the lambs that required minimal assistance on the first day of life from those that were able to suck eventually and from those which were unable to suck successfully before ewes would normally be turned out from the shed.

Comparison of the scores assigned to S (n=424) and SB lambs (n=540) indicated that SB lambs had superior sucking scores than S lambs (medians (with interquartile ranges): S=2 (1.00-2.00), SB=1 (0.00-1.00) $P<0.001$). A higher percentage of SB lambs sucked independently within 2 hours (scores 0 and 1) compared with S lambs (79% and 45% respectively; $P<0.001$; Table 2.4).

In general, lambs which attain poor vigour scores are slow to stand and to suck. Rapid neonatal behavioural development, i.e. progression from birth, through kneel to stand and suck, has been linked to an increase in lamb survival (OWENS *et al.* 1985; DWYER *et al.* 2001; MACFARLANE *et al.* 2009b), where lambs with more vigour and greater sucking ability need less intervention, which reduces the amount of management input required (DWYER and LAWRENCE 2005a). This can only be advantageous for developing a low input system since labour costs are reduced.

The scoring systems developed were derived from lamb data collected from a hill breed and a lowland breed, Scottish Blackface and Suffolk respectively. This resulted in a broad range of categories within the scores, potentially allowing the systems to be used for any breed; different breeds will have different distributions within each of the scoring systems.

2.5.2 Study 2: Validation of the Scoring Systems

2.5.2.1 Lamb Vigour

For each lamb vigour score, given at 5 min of age (Table 2.5), the latencies for lambs to stand, attempt to stand, and kneel differed significantly (i.e. the median latency for a score of 0 was significantly different from the median latency for a score of 1, median latency for score 1 was different from that of score 2 etc). Similarly, the latencies for other behaviours, shake the head ($P=0.037$), kneel ($P<0.001$), and attempt to stand ($P<0.001$), increased significantly as score increased. These results indicate that the vigour score, as a proxy, is able to discriminate between lambs with different rates of behavioural progress after birth.

2.5.2.2 Sucking Assistance

Median lamb latency to suck successfully from the ewe differed significantly between different sucking scores (Table 2.5). Similarly, two behaviours not used to specify the sucking score criteria also differed significantly between the scores (latency to ‘seek udder’, P=0.033, and latency to ‘suck unsuccessfully’, P=0.022). These results indicate that the sucking assistance score is able to discriminate between lambs on the basis of how quickly a lamb progresses to the udder and sucks after birth.

Table 2.5. Score and behavioural latencies recorded simultaneously in cross-bred lambs. Lamb vigour scores are compared using latency from birth to standing. Sucking assistance scores are compared using latency from birth to first successful suck.

Score	Score value	n	Median latency (seconds)	Lower confidence interval	Upper confidence interval	Kruskal Wallis H	*P*
Lamb Vigour	0	4	241.0	207.0	302.0		
	1	19	454.0	362.8	655.0		
	2	100	1074.0	968.0	1224.6	48.60	***
	3	10	1613.0	1241.3	2176.3		
	4	1	977.0	-	-		
Sucking Assistance	0	70	2206.0	1975.2	2446.0		
	1	18	3911.5	2937.5	4503.9	20.07	***
	2	3	3990.0	2101.0	4105.0		

2.5.3 Sensitivity of the Scoring Systems

An important property of a successful scoring system, having been developed using pure-bred lambs, would be the ability to distinguish between the vigour of lambs born to cross-bred ewes and different terminal sires. As anecdotal evidence suggests that Texel-cross lambs (Tx) may be more vigorous than Suffolk-cross (Sx), the sensitivities of the scoring systems were assessed for its ability to discriminate between the scores of Sx and Tx lambs. Analysis of the scores for birth assistance, showed that Sx required a higher level of birth assistance than Tx lambs (Table 2.6; P=0.04). A higher percentage of Texel-cross lambs were born without intervention. Similarly, Tx lambs were significantly more vigorous than Sx lambs (Table 2.6; P<0.001). This effect was also seen in the detailed behavioural data. Latency to stand (Tx v Sx, medians (with interquartile ranges), 768 (482-1099) v 1241 (843-1674) min, P<0.001) and latency to attempt to stand (Tx v Sx, 510 (318-646) v 806 (480-1250), P<0.001) were shorter in Tx than Sx lambs and thus the superior behavioural progress of the Tx lambs compared to Sx lambs was reflected in the scores. Overall, there were no significant differences between genotypes found in the sucking scores (Table 2.6; P=0.247), although only Sx lambs were given the poorest sucking scores (scores 3 and 4; Tx v Sx, 0 v 4, P=0.068). However, Tx lambs sucked more quickly than Sx lambs (Tx v Sx, 2095 v 2734 min, P=0.012) and Tx lambs were also significantly quicker than Sx lambs to seek the udder (Tx v Sx, 1197 v 1663 min, P=0.002) but not to first attempt to suck (Tx v Sx, 1801 v 2186 min, P>0.05).

Table 2.6. χ^2 distribution of scores recorded in cross-bred lambs sired by either Texel or Suffolk rams.

Score		n	0	1	2	3	4	χ^2 *P*
Birth Assistance	**Sx**[1]	78	48	18	5	7	0	*
	Tx[2]	76	56	19	1	0	0	
Lamb Vigour	**Sx**[1]	76	0	5	61	8	2	***
	Tx[2]	75	6	17	45	6	1	
Sucking Assistance	**Sx**[1]	76	44	20	8	2	2	NS
	Tx[2]	76	50	18	8	0	0	

[1] lambs with Suffolk sire; [2] lambs with Texel sire

The scoring systems developed (birth assistance, lamb vigour and sucking assistance) are 5-point categorical scales, ranging from 0-4, allowing an approximately normal distribution of the data (Figure 2.2, 5 minutes of age). This resulted in a system which is sufficiently refined to identify variation between lambs, particularly at the good end of the scale, thus increasing the range of selection possibilities. The majority of the crossbred lambs fell into the middle sections of the distribution resulting in a normal distribution of lamb vigour scores. Table 2.6 indicated that the scores are distributed in a way that would facilitate selection. The sucking assistance score takes into account the different management decisions made by stockmen about how often to assist lambs to suck from the ewes.

The scores developed here for birth assistance and sucking assistance increase as the amount of assistance required increases. This was found, after discussion with farmer groups, to be the most intuitive system to be used by shepherds. To improve the accuracy of on farm data collection, and taking into account requirements from our shepherd focus group, the lamb vigour score was also designed in the same direction such that, for all scores, a higher score indicated a poorer outcome. The lamb vigour scores were developed by analysing an existing database of lamb behaviour, and were thus designed to describe specifically what behaviours lambs were expressing, rather than simply high or low vigour. To reduce any remaining subjectivity within the scores, detailed description/ guidelines of the behaviours associated with the traits are given to the flock owner for data collection on commercial farms.

Several different scoring systems have been used to record levels of dystocia/birth assistance and lamb vigour. Most dystocia scoring systems refer to the amount of human assistance given. SPEAR-SMITH *et al.* (2000) used a categorical 5-point scale which specified the area where the lamb is pulled from, i.e. birth canal or uterus. However, this system is not practical for on-farm data collection requiring detailed recording and did not take into account speed of labour. Other systems have used scales ranging from 1-4; where a score of 1 represents no assistance given, a score of 2 represents slight assistance, a score of 3 represents a difficult birth with manual delivery and a score of 4 represents a difficult delivery or vet assistance (SPEIJERS *et al.* 2010). The birth assistance scoring system developed in this study was similar. However emphasising speed of delivery in the 'no assistance' scores, means that selection for low levels of birth assistance will also result in populations with easier and quicker births and a reduced risk of perinatal hypoxia (HAUGHEY 1993).

Methods for measuring lamb vigour, on the other hand, vary greatly between studies. Several studies have used time-based values, i.e. the latency between birth and standing or appearing to suck (ALEXANDER *et al.* 1990b; BRIEN *et al.* 2009). However, timed behaviour traits are not easy and quick to measure for on-farm when compared to categorical indicator traits (Brien et al. 2009). SPEAR-SMITH *et al.*, (2000) used a vigour score based upon the Apgar score for newborn human infants measured at 1 hour after birth. This 5-point scale ranges from 1, dead; 2, can not stand; 3, minimal vigour; 4, moderate vigour; and, 5, very vigorous. While this score was based upon a lamb's ability to stand, nurse or walk, the score descriptions are vague and the time-scale is not practical for on-farm data collection. The lamb vigour score developed in this study is based upon early lamb behaviour which has been shown to indicate rate of behavioural progression. The time at which this score is taken, 5 minutes after the birth of the lamb, fits well with the management of intensively-housed sheep, minimising disruption to normal management. Similarly, the sucking assistance score is recorded at a time that fits well with good management practice, making the score easy to record.

2.5.4 Effectiveness of scoring systems as selection criteria

Scoring systems are a useful method of quantifying traits that cannot be measured conventionally. For instance, in milk sheep, the milk score relates to the size of the udder immediately after lambing. SNOWDER *et al*. (2001) found that scoring for potential milking (udder size) provided a prediction of a ewe's ability to rear lambs, and could be used for selection. To be able to use a scoring system for selection purposes there must be a high degree of relatedness between the score and the underlying biology. Not all visually scored traits have been found to relate to the underlying linear trait. For example, visually scored carcass conformation has a poor relationship to meat yield (NSOSO *et al.* 2000). For scoring systems to be an effective method of selection, scored traits need standardisation of the categories within them and knowledge of the relationship between scored traits and linear traits (JANSSENS and VANDEPITTE 2004).

2.5.5 Use of Scores in Commercial Farm Situations

The scoring systems are already in use within member flocks of the Suffolk Sheep Society in the UK. Suffolk Sheep Society members have been involved in the score development throughout, with members advising on management practice and the subsequent ease-of-use of the scores. Data gathered from these member flocks have been used in the first study into behavioural genetic parameters in Suffolk sheep, where MACFARLANE *et al.* (2009b) note that the direct heritabilities of birth assistance and lamb vigour are moderate (0.206 and 0.335 respectively), indicating that it would be possible to improve these traits through selection.

2.6 General Implications

In this study we developed a simple on farm behavioural scoring system to collect information on birth assistance and lamb vigour in neonatal lambs, using an experimental flock of two pure-breeds of sheep, with known vigour - Scottish Blackface (hill breed) and Suffolk (lowland breed). The scores were then tested and validated in a second lambing flock, a commercially-kept flock of Scottish Blackface x Border Leicester ewes, mated with either Suffolk or Texel rams, with lambs of unknown vigour. These results showed that the behavioural scoring systems were related to the underlying behavioural responses of the lambs and were sufficiently sensitive to pick out genotype differences between cross-bred lambs. This would indicate that these scoring systems should be a feasible and practical method to measure neonatal lamb vigour to evaluate management systems and to improve selection criteria.

2.7 Conclusions

This study has developed and validated a suite of proxy methods that are suitable for measuring the differences in birth assistance, neonatal lamb vigour and neonatal sucking ability for ewes and lambs in intensive, indoor management systems. These scoring systems combine measurements of human intervention with quantification of behavioural traits and turn them into simple, easy-to-follow scores. The methods are designed to be used within commercial sheep flocks to allow assessment of management changes to improve lambing ease and to aid genetic selection of animals for survival traits within breeding programmes.

CHAPTER THREE

LAMBING EASE AND LAMB VIGOUR CHARACTERISTICS IN LAMBS SIRED BY RAMS OF THREE MAIN SUFFOLK STRAINS

3.1 Abstract

Two main causes of lamb mortality are dystocia and low vigour lambs. Both of these problems can require high levels of human intervention to ensure survival of the lambs. In New Zealand, Suffolks have purportedly been selected for low input ‘easy care’ traits and represent the possibility of introducing genes for improved lambing ease and lamb vigour into the British Suffolk strains. The aim of this study was to compare birth, neonatal behaviour traits and dag scores of lambs sired by rams of three main Suffolk strains.

Welsh Mule ewes were mated with sires from 3 different Suffolk strains: New Zealand sires (NZ) – selected upon ‘survivability’, ease of lambing and performance data, UK High Index-selected sires (UKH) – selected on performance data, or UK Traditional sires (UKT) – unselected. Neonatal records from 665 lambs were obtained, 255 NZ-sired, 205 UKH-sired and 205 UKT-sired. Each lamb was scored for Birth assistance (BA), Lamb vigour (LV, at 10 minutes of age) and Sucking assistance (SA). Birth weights and weight and dag score at 8 weeks of age were also recorded. Score data were ranked and analysed using the Linear Mixed Model procedure in SAS.

There was no significant effect of sire strain on BA rank, but a tendency for NZ-sired lambs to have fewer difficult births than UKH-sired lambs. No difference was found between other Suffolk strains. Lambs that required minor birth assistance were heaviest; however there was no interaction of sire strain and birth weight. There were no significant effects of sire strain on LV rank and SA rank. There were no overall effects of sire strain on birth weight, however, NZ-sired lambs tended to weigh less than those sired by UKH and UKT. This study shows that lambs out of Mules sired by Traditional British and New Zealand rams were similar in performance for birth assistance and lamb vigour traits (LV and SA).

3.2 Implications

Genetic solutions to reduce lamb mortality and its main causes (dystocia and low vigour lambs) are desirable, with the added benefit of a reduction in the labour-input required during parturition. At least two possible genetic solutions are available: (i) use of suitable breeds or strains and (ii) intrabreed selection. Approach (i) requires the existence of breed/strain differences in the desired traits and approach (ii) needs sufficient intrabreed genetic variance. With discussed caveats, this study has not provided sufficient evidence to support approach (i), however related studies (for example, MATHESON *et al.* 2010) show a high feasibility for approach (ii).

3.3 Introduction

Lamb mortality remains a significant welfare and production issue for the sheep industry (HAUGHEY 1993). Dystocia and poor lamb vigour are significant contributors to lamb mortality, with mortality rates being highest within the first 3 days of postnatal life (NOWAK *et al.* 2000; SAWALHA *et al.* 2007). In intensive systems, lamb mortality during parturition and the neonatal period is minimised through supervision and assistance, resulting in investment of labour to ensure lamb survival (FISHER 2003). Substantial human input can be required to assist with difficult parturitions and in ensuring that lambs suck quickly after birth in these systems (DWYER and LAWRENCE 2005a).

Low input management systems are becoming more common, due to a decrease in farm incomes and subsidy payments. As farmers attempt to reduce labour costs, the number of sheep managed per stockperson is increased (CONINGTON *et al.* 2010). To achieve a lower input system, without impacting upon welfare, lambs need to be delivered easily, be active, vigorous and able to suck from their mothers unaided (DWYER and LAWRENCE 2005a). Therefore, selection for survival and welfare traits reducing levels of required input is desirable. Previous studies have shown improvement in lamb survival through selection (KILGOUR and HAUGHEY 1993; CLOETE *et al.* 2009), and demonstrate the possibility of selection for improved neonatal behaviours, requiring reduced levels of human intervention. Additional to this intrabreed selection, there is the opportunity for genetic improvement by introgressing suitable genes from other strains or breeds, which have been already selected for these traits. Both opportunities depend on a sufficient magnitude of genetic variation.

The presence of genetic variation in neonatal behaviour traits is well-documented, for example, studies have shown breed differences in neonatal lamb behaviours (DWYER and LAWRENCE 2005b; DWYER 2008b), line differences within single breeds (DWYER *et al.* 2001; CLOETE *et al.* 2002), and sire effects within breed (DWYER *et al.* 2005). In addition, differences have been found in neonatal behaviours between terminal sire cross-bred lambs (Suffolk and Texel; MATHESON *et al.* 2011). Terminal sire breeds have repeatedly been shown to have poorer lamb vigour than maternal hill breeds, (DWYER and LAWRENCE 2000; DWYER and LAWRENCE 2005a; DWYER 2008a), however, there is great deal of variation in lamb vigour present within terminal sire breeds.

Indeed, when Suffolk-cross lambs were compared to cross-bred lambs from other terminal sire breeds (Southdown, Hampshire Down, Texel and Corriedale), Suffolk-cross lambs had a higher percentage of mortality at birth and required more assistance at birth than other crosses (BIANCHI *et al.* 2001). Lamb survivability and the amount of human assistance required by the Suffolk breed are of importance to commercial producers who purchase a pure-bred sire for use on cross-bred ewes to produce cross-bred slaughter lambs. Improving lambing ease and lamb vigour at birth would help achieve a low input system without compromising ewe or lamb welfare.

In New Zealand the Suffolk breed has purportedly been selected for low input ‘easy care’ traits and provides the possibility of introgressing genes for improved lambing ease and lamb vigour into the British Suffolk strains. However, there has been no published record of how much 'NZ genetics' would improve (or compare to) British Suffolks under standard UK management practises. Therefore, the objectives of this study were to examine possible differences in neonatal behavioural traits (birth assistance, lamb vigour and sucking assistance) between NZ and UK Suffolks when used as terminal sires on commercial cross-bred ewes.

3.4 Material and Methods

3.4.1 Animals

Welsh Mule ewes were synchronised in oestrus and mated, via artificial insemination (AI), with sires from 3 different strains: New Zealand sires (NZ, n=4, all ram lambs), UK High Index-selected sires (UKH, n=3, 1 one-year-old, 1 two-year-old and 1 mature ram), or UK Traditional sires (unselected; UKT, n=3, all ram lambs). The NZ strain has been selected through culling of animals with traits requiring extra labour, and through performance recording, in New Zealand. The UK Suffolk Selection Index combines estimated breeding values for recorded traits (for instance, 8 and 21 week live weight, muscle and fat depth measured via ultrasound and mature live weight) into a single value, allowing ranking of sires. The higher the Index value of the sire, the more suitable the ram is for the objective defined by the Index. UK Traditional sires were selected on the basis of conformation by sight. The NZ and UKH rams were sourced from IBERS and Innovis, while the UKT rams were borrowed from Suffolk Sheep Society members. All rams were trained at Innovis' Aberystwyth Centre for up to 4 days prior to semen collection (to ensure good semen quantity and quality for AI).

In total, 506 ewes were divided into three groups of 160-170, balanced for age (2-4 years old). Ewes were artificially inseminated (AI) in two batches one week apart. After insemination, all ewes were run as one flock with any ewes returning to service mated with Texel rams, to ensure known parentage of the lambs. Ewes were group housed approximately 6 weeks prior to lambing, in commercial-sized straw-bedded pens, irrespective of sire strain and according to scanned litter size. Silage was available *ad libitum* and concentrates fed according to the intrauterine litter size, measured by ultrasound scanning in early pregnancy. Observers were present for 24 h a day during lambing. All ewes were allowed to give birth unaided, as far as possible, according to a standard lambing protocol. The protocol permitted assistance if the birth process failed to progress, i.e. if no lamb parts were seen 1 h after the appearance of fluids and/or 2 h after lamb parts had been seen with no other obvious progress. Any intervention was kept to a minimum. Certain specific presentations (breech, head back and two lambs together) required immediate assistance.

Each lamb was scored on birth assistance (BA), lamb vigour at 10 minutes of age (LV) and sucking assistance (SA; Table 3.1). The neonatal scores used were based on those earlier described (MATHESON *et al.* 2011). As well as score data, latencies from birth to performing specific behaviours (Table 3.2) were collected where possible. Latencies were recorded from time of birth (using a stopwatch) to the time at which a specific behaviour first occurred. Birth weight (BWT) of the lamb was also recorded within 12 hours of birth. Ewes and lambs were moved to individual 1.2m x 1.2m straw-bedded 'mothering' pens after the 10 minute vigour score (or within 2 h of birth if latencies were being recorded). Ewes and lambs stayed in the individual pens for approximately 24 after lambing, when they were turned out to pasture, assuming no complications and if the lambs were sucking unaided. *Ad libitum* access to silage and clean fresh drinking water were available in the individual pens and ewes were fed concentrate mix to meet energy requirements. All recording was done blind to the knowledge of lamb sire.

Table 3.1. Definitions of birth assistance scores, lamb vigour scores and sucking assistance scores.

(a)	**Birth assistance scores**
1	Unassisted or easy uncomplicated delivery
2	Minor assistance required. Presentation corrected, little effort needed to deliver lamb
3	Major assistance required. Difficult delivery needing effort to deliver lamb
4	Veterinary assistance required

(b)	**Lamb vigour scores** (at 10 minutes of age)
0	Extremely active and vigorous lamb, has been standing on all 4 feet
1	Very active and vigorous lamb, standing on back legs and on knees
2	Active and vigorous lamb, on chest and holding head up
3	Weak lamb, lying flat, able to hold head up
4	Very weak lamb, unable to lift head, little movement

(c)	**Sucking assistance scores**
0	Lamb sucking well without assistance within 1 h of birth
1	Lamb sucking well without assistance within 2 h of birth
2	Lamb given sucking assistance/ fed by stomach tube once or twice in first 24 hours after birth
3	Lamb given sucking assistance, fed by stomach tube more than twice, needing help after 1 day old, but able to suck by 3 days old
4	Lamb still needing help to suck when more than 3 days old

Table 3.2. Ethogram of neonatal lamb behavioural progression. Latencies are measured as the time from birth to when specific behaviours are first displayed.

Behaviour	Definition
Shake Head	Lamb lifts its head off the ground and shakes its head from side to side
Kneel	Lamb is lying on its chest, and pushes its chest off the ground supporting some of its weight on the knees
Attempt to Stand	Lamb supports its weight on one or more hind legs while balanced on the knees of the front legs, duration must last for at least 5 seconds
Stand	Lamb supports its weight on all four legs, duration must last for at least 5 seconds
Seek the Udder	Lamb must actively move towards the udder area and have its nose/mouth within 10 cm of the ewes teat area
Unsuccessful Suck	Lamb has hold of the teat but either lets go of the teat or the ewe moves away causing the lamb to let go, lamb will usually be moving
Successful Suck	Lamb latches onto teat, lamb may make sucking noises and/or waggle its tail, lamb will usually stand still

3.4.2 Statistical methods

Of the 506 ewes programmed for AI, 488 were successfully inseminated. Eighteen ewes lost their ear tags between AI and lambing and were, therefore, excluded from analysis. In total, there were 702 lambs born from 333 ewes, neonatal score recordings were made on 665 lambs (255 NZ, 205 UKH, 205 UKT), and latency data were recorded for 226 lambs (98 NZ, 60 UKH, 68 UKT).

Score data were ranked and latency data were log transformed to normalise the data. Rank transformation normalises the residuals of ordinal data as much as possible, allowing the use of linear models and estimation of fixed effects (CONOVER and IMAN 1981; WEISS 1986); this approach has also been used in previous studies using score data, for example ROOKE *et al*. (2009). The tied rank values for all categories of scores are shown in table 3.3. Both transformed score data and transformed latency data were analysed using the Linear Mixed Model procedure in SAS 9.1.3 (2006). Sire strain analyses included: sire strain (3 levels), ewe age (3 levels), lamb sex and litter size (4 levels) as fixed effects and sire ID fitted as a random factor nested within sire strain, and ewe ID as a random factor. In addition, BA score had BWT as a covariate**;** LV score had BA and BWT; SA score had BA, LV and BWT. Sire ID analyses were performed on subsets based on sire strain with sire ID as a fixed effect and ewe ID as a random effect. For ease of understanding, the score rank results were then back-transformed into the same scale as the original scoring system using logistic regression. For each score, the regression coefficients were close to 1. The relative rank for individual sires within each scoring system was determined by ranking each sire from those with the lowest cumulative score (rank 1) to those with the highest (rank 10). The overall neonatal rank was decided by summing the ranks with each of BA, LV and SA, in ascending order with overall neonatal rank 1 for the sire with the lowest overall total.

Table 3.3. Tied rank* value for each category for: birth assistance, lamb vigour and sucking assistance.

Trait	Score category				
	0	1	2	3	4
Birth assistance tied rank value	-	224.5	527.5	625.5	650
Lamb vigour tied rank value	64.5	190	381.5	523	536
Sucking assistance tied rank value	176	421.5	508	-	-

*The ranking procedure gives the same rank to duplicate values and resumes ranking for subsequent numbers after leaving a gap in the numbering.

3.5 Results

3.5.1 Sire strain analysis

There were no significant overall effects of sire strain on birth weight (Table 3.4), however, NZ-sired lambs tended to be ~5% lighter than UKH (P=0.070) and UKT (P=0.071). There was also no significant difference in birth weight at the individual sire level. There was no significant overall effect of sire strain on the levels of BA needed (Table 3.4), however, NZ-sired lambs tended to have fewer difficult births than UKH-sired lambs (*P*=0.089) but no difference was found between lambs sired by NZ and UKT nor between UKT and UKH. At the individual sire level, there was no overall effect on the proportion of lambs requiring assistance or on the levels of BA required.

Table 3.4. Least square means ± standard error (with back-transformed values using logistic regression in parentheses), at the sire strain level, for birth weight and ranks of the three neonatal behaviour scores (birth assistance, BA, lamb vigour, LV, and sucking assistance, SA; for all the scores, a lower rank indicates a better score).

	Trait			
Sire strain	Birth weight	BA rank	LV rank	SA rank
NZ	4.43 ± 0.13	306.3 ± 21.2 (1. 25)	298.0 ± 24.3 (1.56)	326.8 ± 24.1 (0.56)
UKH	4.65 ± 0.14	338.4 ± 22.2 (1. 49)	295.7 ± 25.3 (1.37)	304.1 ± 25.3 (0.48)
UKT	4.64 ± 0.14	316.9 ± 22.4 (1. 28)	271.8 ± 25.6 (1.43)	310.9 ± 25.1 (0.50)
F value	3.10	1.99	1.20	0.99
P	*P*>0.05	*P*>0.05	*P*>0.05	*P*>0.05

There were no significant effects of sire strain on LV rank and SA rank (Table 3.4), with no differences found between any of the sire strains. However, there was a significant variation between individual sire in the levels of LV of their progeny (P= 0.027). For the in-depth behavioural latency data, there were no effects of sire strain, or individual sire, on the latency to shake the head, kneel, attempt to stand and stand; there were also no effects of sire strain on the latencies to seek the udder and to the first successful sucking attempt (data not shown). To get individual sire rankings, for each neonatal trait (BA, LV and SA), the scores were added together for each individual sire (A-J). Sires were then ranked from 1-10, with 1=lowest total sum of scores and 10=highest total sum of scores. The rankings for each neonatal trait are shown in Table 3.5, with the overall neonatal ranking being the sum of all the traits.

The rankings for each sire indicate that there is more variation between sires than between sire strain.

Table 3.5. Sire ranking for the neonatal traits birth assistance (BA), lamb vigour (LV) and sucking assistance (SA) with the overall neonatal ranking.

		Trait			Neonatal
Sire ID	Sire strain	BA	LV	SA	ranking
A	NZ	3	10	4	**5**
B	NZ	2	5	9	**4**
C	NZ	5	6	5	**4**
D	NZ	4	4	10	**6**
E	UKH	9	7	1	**5**
F	UKH	10	9	7	**8**
G	UKH	6	3	3	**3**
H	UKT	8	8	6	**7**
I	UKT	7	1	2	**1**
J	UKT	1	2	8	**2**

3.5.2 Fixed effects on neonatal scores

Lambs born in large litters required greater levels of BA than those born in smaller litters (Table 3.6). There were no effects of litter size on LV or SA. Single lambs were heavier than twins and other multiples. Lamb sex had no effect on the amount of BA needed (Table 3.6), nor were there any effects of sex on LV or the amount of SA required. Male lambs were 300 g (6.7%) heavier at birth than females. There was no effect of ewe age on the amount of BA or SA needed, nor was there any relationship between dam age and LV (Table 3.6). Dam age was a significant factor for lamb birth weight, with older ewes giving birth to heavier lambs than younger ewes.

Table 3.6. The effect of litter size on birth weight (BWT), birth assistance rank (BA rank), lamb vigour rank (LV) and sucking assistance rank (SA rank), shown as least square means ± standard errors (with back-transformed values using logistic regression in parenthesis). Within a column, means without a common superscript differ (P < 0.05).

		Trait			
Litter size at birth	N	BWT (kg)	BA rank	LV rank	SA rank
1	91	5.98 ± 0.16 [a]	301.7 ± 27.5 (1.23) [a]	291.6 ± 31.1 (1.53) [a]	317.0 ± 29.8 (0.53) [a]
2	371	4.85 ± 0.15 [b]	267.1 ± 23.9 (1.13) [a]	301.8 ± 26.4 (1.58) [a]	330.4 ± 26.6 (0.58) [a]
3	154	3.87 ± 0.17 [c]	280.1 ± 27.8 (1.17) [a]	268.4 ± 30.1 (1.42) [a]	354.0 ± 30.5 (0.67) [a]
4	7	3.59 ± 0.42 [c]	433.5 ± 67.9 (1.63) [b]	292.2 ± 67.9 (1.54) [a]	254.4 ± 63.4 (0.30) [a]
F value		91.25	2.70	1.02	1.13
Significance		<0.001	0.046	*P*>0.05	*P*>0.05
Lamb sex	N	Birth weight	BA rank	LV rank	SA rank
F	296	4.42 ± 0.13	314.2 ± 21.0 (1.27)	280.2 ± 23.8 (1.48)	308.4 ± 23.9 (0.49)
M	321	4.72 ± 0.12	327.0 ± 20.2 (1.31)	296.8 ± 22.9 (1.56)	319.5 ± 22.8 (0.54)
F value		20.60	1.38	1.83	1.34
Significance		<0.001	*P*>0.05	*P*>0.05	*P*>0.05
Dam age (years)	N	Birth weight	BA rank	LV rank	SA rank
2	128	4.17 ± 0.15 [a]	313.6 ± 24.3 (1.27) [a]	305.6 ± 27.4 (1.61) [a]	320.9 ± 26.6 (0.54) [a]
3	264	4.57 ± 0.13 [b]	322.4 ± 21.0 (1.29) [a]	277.9 ± 23.6 (1.46) [a]	324.4 ± 24.3 (0.56) [a]
4	238	4.97 ± 0.13 [c]	325.7 ± 21.4 (1.30) [a]	282.0 ± 24.1 (1.48) [a]	296.6 ± 24.5 (0.45) [a]
F value		25.60	0.20	1.00	1.84
Significance		<0.001	*P*>0.05	*P*>0.05	*P*>0.05

3.6 Discussion

This study demonstrates that UKT-sired lambs and NZ-sired lambs were similar in performance for the frequency and severity of required birth assistance. Whilst UKH-sired lambs tended to require slightly greater levels of assistance at birth when compared with NZ-sired lambs, the differences were not statistically significant. No strain differences were found in the neonatal lamb vigour traits, lamb vigour and sucking assistance. Increased birth weight is known to increase the likelihood of dystocia, possibly due to increased flexion of the shoulder and elbow flexion (GROMMERS *et al.* 1985) or reduced uterine space for manoeuvring during parturition (FRASER and TERHUNE 1977). In this study, UKH-sired and NZ-sired lambs differed slightly in lamb birth weight, which might account for the small difference between the strains in birth difficulty. However, birth weight was added as a covariate in the model used to calculate birth assistance. Thus the results obtained should be independent of lamb birth weight, although other factors, such as skeletal conformation, may also influence birth assistance.

The main fixed effects of lamb sex, litter size at birth and ewe age were all similar to those reported in other studies on neonatal lamb traits. For instance, NAWAZ and MEYER (1992) showed that male lambs required more assistance at birth than female, an effect that persisted even after birth weight was added as a covariate in the analysis; while OWENS *et al* (1985) and DWYER (2003) showed that birth weight decreases with litter size and that younger ewes had lighter lambs than older ewes. Birth assistance score was most affected by the birth weight of the lamb and the litter size at birth. Nevertheless, the results for individual sire differences in lamb vigour were independent of the amount of birth assistance that was required. Similarly, the results for individual sire differences in sucking assistance were independent of both the amount of birth assistance that was required and the vigour of the lamb at 10 minutes after birth.

The data suggests, in agreement with a previous study (DWYER *et al.* 2005), that significant variation exists between sires within breed in neonatal behavioural traits (with reference to the ranking of sires). However, individual sires which had good results in one neonatal trait were not consistent across all neonatal traits (Table 3.4). The sires with the best overall neonatal rankings were Traditional (UKT; rankings 1 and 2) and High Index-Selected (UKH; rank 3). Neither of the top 2 ranking sires were consistently good across all traits; the sire ranked 1st was very good for lamb vigour and sucking assistance but was one of the worst for birth assistance; the sire ranked 2nd was very good for birth assistance and lamb vigour but was one of the worst for sucking assistance. A similar trend is seen in all the sires and shows the range of variation within traits that is available for selection in a breeding programme. This would be indicative for lower genetic correlation between these traits and suggests that all traits might be required in a selection index. However, in contrast with this study, recent genetic parameter studies on pedigree Suffolk sheep have indicated that there are moderate genetic correlations between the neonatal traits (MACFARLANE *et al.* 2010b; MATHESON *et al.* 2010).

A criticism which may be levelled at this study is that categorical scoring systems are not capable of discerning differences between strains/genetic lines. However, the scoring system used in this study was sensitive enough to detect the impact of sire genotype on the vigour of cross-bred lambs (MATHESON *et al.* 2011) and has been able to discern sire differences within this study. However, although differences in lamb vigour between pure breeds are well-documented (DWYER and LAWRENCE 2000), there are few studies into sire effects in progeny of cross-bred dams when a positive effect of heterosis may be expected. For example, FLINN and WHITEMAN (1974) found no significant difference in lamb vigour between Scottish Blackface sires and Dorset sires when mated with a composite ewe breed designed to maximise reproductive efficiency. In contrast, a significant effect of sire on neonatal lamb vigour traits in Scottish Blackface, Suffolk or their reciprocal crosses has been found (C. DWYER, unpublished). Therefore, there was no reason to suspect that the vigour scoring system used in the present experiment was not sensitive enough to distinguish meaningful differences in lamb vigour between the strains.

Studies into the genetics of birth assistance and neonatal lamb vigour traits in the general Suffolk population have reported heritabilities of 0.21±0.053 for birth assistance and 0.33±0.141 for lamb vigour (MACFARLANE *et al.* 2010b), conducted on 1520 lambs born in 2006. A more recent study, involving a larger number of lambs (approx 17,000), and using a more refined scoring system, have reported heritability estimates of 0.27±0.034, 0.34±0.037 and 0.19±0.031 for birth assistance, lamb vigour and sucking assistance respectively (MATHESON *et al.* 2010). These studies show that the neonatal behavioural traits used in this present trial are highly heritable. However, even with heritabilities this high, the number of sires used, and lambs available, in the current comparative Suffolk study are relatively low and, as such, may not fully reflect the variation within the broader strain populations. A future experiment with a greater number of sires (and lambs) from each strain will provide more information. Additionally, one could expect larger strain differences in pure-bred lambs, as crossbred have only 50% of the purebred genes, maternal breed effects could be important and this would remove any possible positive effects of heterosis via dilution. However, the effect in crossbred lambs is of larger relevance to the UK industry as most slaughter lambs will be produced out of mules.

3.7 Conclusions

This comparative study into neonatal behaviour traits in the crossbred progeny of New Zealand, High-Index and Traditional UK Suffolk rams found little difference at the sire strain level in terms of the likelihood of requiring birth assistance. However, lambs sired by High-Index Suffolk rams tended to require more assistance at birth and have more difficult births than NZ sired lambs. There was no difference in lamb vigour and sucking assistance between the three sire strains. Individual sire differences in lamb vigour and sucking assistance and the magnitude of reported heritabilities in other studies for these traits indicate that there is sufficient genetic variation present in the wider UK Suffolk population to improve neonatal traits through careful selection. These traits should thus be included in future breeding goals/selection indexes.

CHAPTER FOUR

GENETIC PARAMETERS FOR BIRTH ASSISTANCE AND LAMB VIGOUR TRAITS IN A PURE-BRED TEXEL POPULATION ACCOUNTING FOR TEXEL DOUBLE MUSCLING QTL (TM-QTL) GENOTYPES

4.1 Abstract

The Texel double-muscling QTL (TM-QTL) has been reported to increase muscle depths in certain carcass traits. However, it is unknown whether TM-QTL has any effect on neonatal lamb welfare and behaviour traits. Therefore, the aim of this study was to estimate the effects of TM-QTL genotype on the amount of birth assistance needed (BA), perinatal lamb vigour score (LV) and amount of sucking assistance needed (SA) and to estimate genetic parameters for these neonatal traits to evaluate selection opportunities. Results show that lambs inheriting one or two copies of TM-QTL, from either sire or dam, require more SA than homozygous wildtype lambs. To our knowledge this is the first report of an impact on lamb behavioural traits associated with carrying a muscling QTL in sheep. Heritabilities for all the measured neonatal traits range from low-moderate, BA 0.43 (s.e. 0.063), LV 0.15 (s.e. 0.059), SA (0.27 (s.e. 0.045), suggesting there is sufficient genetic variation present within the Texel population to allow selection for improved neonatal welfare and behaviour traits, whilst accounting for the differential effects of TM-QTL.

4.2 Introduction

High levels of lamb mortality are a significant welfare issue in sheep production (15-25% of lambs die before weaning worldwide), with mortality rates highest within the first 3 days of postnatal life (NOWAK *et al.* 2000; SAWALHA *et al.* 2007). Lamb survival is to a degree dependent upon an easy delivery and the expression of appropriate behaviours from both mother and offspring, such as rapid standing, udder-seeking and sucking by the lamb (DWYER and LAWRENCE 2005b). Neonatal lambs have well-adapted behaviour patterns that come into action immediately after birth (NOWAK and POINDRON 2006), and lambs need to be vigorous in order to rapidly seek the udder, find the teat and suck.

Lamb vigour can be defined as the rate of the progression of neonatal behaviours immediately after birth, i.e. the lamb is born, learns to stand and seek out the udder, culminating with a successful sucking bout. A low vigour lamb will take longer to complete this behavioural progression than a lamb with higher vigour. Slow behavioural progression may have several consequences for the lamb: lambs slow to stand and suck are at risk of depleting their energy reserves (NOWAK and POINDRON 2006), developing hypothermia (GROMMERS *et al.* 1985; DWYER and MORGAN 2006; POLLARD 2006) and reduced absorption of immunoglobulins (NOWAK and POINDRON 2006) and may have impaired mother-young bonding (NOWAK *et al.* 1997; DWYER *et al.* 2003; NOWAK *et al.* 2007), resulting in poor maternal care and early lamb death (Nowak 1996).

Although there are few studies into the behavioural genetics of sheep, breed and line differences are often considered as evidence of genetic variation (HINCH 1997). Breed differences in udder-seeking behaviours have been found in both pure-bred and cross-bred lambs (STEVENS *et al.* 1984; SLEE and SPRINGBETT 1986; O'CONNOR and LAWRENCE 1992). Line and sire within breed effects on neonatal behaviours have also been found (DWYER *et al.* 2001; CLOETE *et al.* 2002). In addition to any breed or sire differences, indicative for genetic variance, there are also successful lamb survival selection experiments that have been carried out proving that there is sufficient within breed variance for selection (KNIGHT *et al.* 1988; KILGOUR and HAUGHEY 1993;

CLOETE and SCHOLTZ 1998). These indicators suggest there is an evident genetic basis for lambing difficulty and neonatal lamb vigour traits.

Genetic solutions are cost-efficient, cumulative, permanent and sustainable and have the potential to improve birth assistance and lamb behaviour traits. However, relatively large amounts of data are needed to accurately estimate genetic parameters (FAURE 1994). Although behavioural traits are often difficult to measure in a timely manner on farm, simple, proxy methods (scoring systems) have been developed to assess levels of birth difficulties and lamb vigour (MATHESON *et al.* 2011). These scores were developed for the purpose of selection, allowing for data collection on farm and enabling mass phenotyping, potentially resulting in large amounts of data (see, for example, genetic parameters for neonatal traits in Suffolk sheep; MACFARLANE *et al.* 2010b; MATHESON *et al.* 2010).

The sheep industry is increasingly using breeding to improve production traits (Simm et al. 2001), either through the use of selection-indexes and/or genetic markers for quantitative trait loci (QTL) or known genes, with their potential for faster improvements. One QTL recently found is the Texel muscling QTL (TM-QTL), found on ovine chromosome 18 (WALLING *et al.* 2004; MATIKA *et al.* 2006), and affects loin muscle growth. The QTL exhibits a polar overdominant mode of inheritance, with paternally expressed imprinting (MACFARLANE *et al.* 2010a), thus resulting in an increased effect when the QTL is inherited from the sire. The effects of TM-QTL appear to be restricted to the loin area, affecting loin shape and increasing muscle area, weight and depth, and are expressed with similar magnitude in pure-bred and cross-bred animals (MACFARLANE *et al.* 2009a). It would, therefore, be advantageous for producers to incorporate TM-QTL into their flocks. However, if TM-QTL is to be used in commercial sheep breeding programmes, there needs to be evidence that neonatal health and welfare traits are not adversely affected (MACFARLANE *et al.* 2010a).

Thus, the objective of this study was to: (i) determine the effects of TM-QTL carrier status on neonatal behaviour traits (birth assistance, lamb vigour and sucking assistance); and, (ii) estimate the heritabilities of those traits and the correlations between them. We analysed data from a sub-population of 799 pure-bred Texel lambs born over 2 years. Using univariate phenotypic analysis, we tested the hypothesis that possession of a TM-QTL genotype negatively affects neonatal behaviour and welfare traits. Using multivariate analysis, heritabilities, genetic and phenotypic correlations were obtained to determine the variation available for selection in neonatal traits.

4.3 Materials and Methods

4.3.1 Animals

All procedures involving animals were approved by the Scottish Agricultural College (SAC) Animal Ethics Committee and were performed under UK Home Office licence, following the regulations of the Animals (Scientific Procedures) Act 1986. Data were collected in the years 2008-2009 from a population of Texel sheep from two farms (SAC, Scotland, and IBERS, Wales). This Texel population has been managed to increase the frequency of heterozygous TM-QTL carriers and to produce some homozygous carriers. Eight sires (of known TM-QTL status) and 312 dams (of both known and unknown genotype) produced lambs which were subsequently genotyped for TM-QTL status following the procedure outlined earlier MACFARLANE *et al*. (2009a). In total, data were collected from 799 lambs: 368 male, 431 female; 297 singles, 410 twins, 88 triplets (2 lambs were considered too weak and were removed from the study) and 4 quadruplets. After genotyping, 196 lambs had known TM-QTL status, leaving 603 with unknown or only partially known status. Classification of genotype is as follows: $+^S/+^D$: homozygous non-carrier; $+^S/TM^D$: heterozygous carrier with TM-QTL inherited from the dam; $TM^S/+^D$: heterozygous carrier with TM-QTL inherited from the sire; TM^S/TM^D, homozygous carrier.

4.3.2 Ewe and lamb management

Ewes were group-housed in straw-bedded large pens prior to lambing, and were fed a concentrate diet and *ad libitum* hay to satisfy 100% nutrient requirements. Observers were present 24 h a day during lambing to record births. All ewes were allowed to give birth unaided, as far as possible, according to a standard lambing protocol (DWYER and LAWRENCE 1998). The protocol permitted assistance if the birth process failed to progress, i.e. if no parts of the lamb were seen 1 h after the appearance of fluids and/or 2 h after parts had been seen with no other obvious progress. Any intervention was kept to a minimum, correcting presentational difficulties where possible before allowing the ewe to continue unaided. Certain specific presentations (breech, head back and two lambs together) required immediate assistance. After birth ewes and lambs were moved to individual ‘mothering-up’ pens. Ewes and lambs remained indoors for the first 3 days after birth and were then turned out to permanent pasture.

4.3.3 Data collection

Scoring systems, based on lamb behavioural development, have been developed for birth assistance, lamb vigour and sucking assistance (Table 4.1; MATHESON *et al.* 2011). The scoring systems are accompanied by comprehensive guidelines to minimise the subjectivity of the scores. Each lamb was scored on whether they needed assistance at birth (Assisted; 0/1 score; 0 = no assistance, 1 = assistance needed), the amount of birth assistance (BA), lamb vigour (LV, at 5 minutes of age) and sucking assistance (SA). The number of lambs allocated to each category of scores is given in Table 1. In addition, lamb sex, litter size the lamb was born into and birth weight were also recorded within 2 hours of birth.

Table 4.1. Definitions of birth assistance scores, lamb vigour scores and sucking assistance scores and lamb distribution within the scores

(1)	**Birth assistance scores**	**Number of lambs**
0	Unassisted or easy uncomplicated delivery of short duration (<30 minutes)	265
1	Unassisted or easy uncomplicated delivery of longer duration (>30 minutes)	80
2	Minor assistance required. Presentation corrected, little effort needed to deliver lamb	349
3	Major assistance required. Difficult delivery needing effort to deliver lamb	89
4	Veterinary assistance required	16
(2)	**Lamb vigour scores** (at 5 minutes of age)	
0	Extremely active and vigorous lamb, has been standing on all 4 feet	43
1	Very active and vigorous lamb, standing on back legs and on knees	280
2	Active and vigorous lamb, on chest and holding head up	399
3	Weak lamb, lying flat, able to hold head up	69
4	Very weak lamb, unable to lift head, little movement	8
(3)	**Sucking assistance scores**	
0	Lamb sucking well without assistance within 1 hour	189
1	Lamb sucking well without assistance within 2 hours	398
2	Lamb given sucking assistance/ fed by stomach tube once or twice in first 24 hours after birth	172
3	Lamb given sucking assistance, fed by stomach tube more than twice, needing help after 1 day old, but able to suck by 3 days old	31
4	Lamb still needing help to suck when more than 3 days old	9

4.3.4 Statistical analysis

Phenotypic analyses of the fixed effects were performed using the Linear Mixed Model procedure in SAS (SAS version 9.1.3, 2006). The baseline fixed effects used in the phenotypic analyses were: farm-year management group (3 levels), age of dam (7 levels), lamb sex (male and female), litter size the lamb was born to (4 levels), lamb TM-QTL status (4 levels). Additionally, birth weight was included as a linear covariate for the analyses of Assisted, BA, LV and SA; birth assistance score was included for analysis of LV and SA; and, lamb vigour score was included for analysis of SA. For the purposes of estimating the effects of TM-QTL genotype on neonatal traits only the subset of lambs with known TM-QTL's was analysed (n=196). For all other fixed effects, the full dataset with 799 lambs was used to account accurately for fixed effects for genetic analysis. The full data set of 799 lambs also had an interaction between birth weight and TM-QTL status included in the model. Whether a lamb needed assistance or not (Assisted) was analysed using the Maximum Likelihood Ratio χ^2 procedure in SAS to allow for small group sizes..

All genetic parameters, genetic and phenotypic correlations for the neonatal traits (BA, LV and SA) were obtained using a 3-variate model, containing 799 animal records, using ASReml (GILMOUR *et al.* 2006). The pedigree file contained 1,727 animals with 799 records available for neonatal traits (BA, LV and SA) and birth weight. Univariate and bivariate models were used to construct the final trivariate model used. The fixed effects used in the genetic analysis were: farm-year management group, age of dam, lamb sex, litter size the lamb was born to, lamb TM-QTL status and a linear covariate of birth weight. Random effects were direct additive and the environmental effect of the litter along with the residual. The environmental effect of the litter was used to account for some dams producing lamb more than one lamb in one year. The data used only covered 2 years and, as such, it was not possible to separate maternal additive effects, maternal permanent environmental effects and temporary environmental effects for any of the traits. The ratio of maternal effect (referred to as ‘the permanent environmental effect of the litter’) to phenotypic variance (σ_{pe}^2) was also calculated for each trait.

4.4 Results

4.4.1 TM-QTL Genotype analysis

Overall, there was a significant effect of TM-QTL on birth weight of the lambs (Table 4.2**;** F test = 3.79; *P*=0.013). Lambs which had inherited a copy of the QTL from the sire (either $TM^S/+^D$ or TM^S/TM^D) weighed significantly more than lambs which only inherited the QTL from the dam ($+^S/TM^D$). The birth weight of non-carrier lambs ($+^S/+^D$) did not differ from either heterozygous or homozygous lambs. There was a tendency for genotype to have an effect on the whether a lamb was Assisted at birth (Likelihood ratio χ^2 = 6.72; *P*=0.083). There was no effect of TM-QTL on the amount of BA needed or LV at 5 minutes of age (F test = 0.71; *P*>0.1; and F test = 0.93; *P*>0.1, respectively). There was, however, a significant effect of genotype on the amount of SA needed (F test = 3.79; *P*=0.013). Lambs heterozygous or homozygous for the TM-QTL required more assistance to suck than non-carriers although only the difference for $TM^S/+^D$ and TM^S/TM^D lambs was significant (Table 4.2). There was a significant interaction of birth weight x TM-QTL on the amount of SA needed (*P*=0.051).

Table 4.2. Mean (± standard error) for all traits measured at birth for known TM-QTL genotypes[1,2,3]. Maximum Likelihood Ratio χ^2 for whether a lamb needed assisted or not at birth. Values are given as actual observations (expected observations).

	TM-QTL				
Trait	$+^S/+^D$	$+^S/TM^D$	$TM^S/+^D$	TM^S/TM^D	***P***
N	52	25	74	45	
Birth weight	3.80 ^{ab} ± 0.23	3.48 ^{a} ± 0.25	3.93 ^{b} ± 0.20	3.97 ^{b} ± 0.21	*
Birth assistance	0.89 ^{a} ± 0.35	1.00 ^{a} ± 0.38	1.17 ^{a} ± 0.33	0.96 ^{a} ± 0.36	NS
Lamb vigour	1.43 ^{a} ± 0.29	1.57 ^{a} ± 0.31	1.61 ^{a} ± 0.27	1.74 ^{a} ± 0.29	NS
Sucking assistance	1.27 ^{a} ± 0.27	1.60 ^{ab} ± 0.29	1.68 ^{b} ± 0.26	1.61 ^{b} ± 0.29	**
Not assisted at birth	20 (19.4)	13 (9.3)	20 (27.6)	20 (16.7)	†
Assisted at birth	32 (32.6)	12 (15.7)	54 (46.4)	25 (28.2)	

†*P* < 0.10, **P* ≤0.05, ***P* ≤ 0.01, ****P* ≤ 0.001

[1]TM-QTL legend: $+^S/+^D$ = homozygous non carrier; $+^S/TM^D$ = heterozygous carrier, inherited from the DAM; $TM^S/+^D$ = heterozygous carrier, inherited from the SIRE; TM^S/TM^D = homozygous carrier

[2] Means within a row sharing a common superscript are not significantly different (*P* > 0.05)

[3] Lambs with unknown/partially known genotype (n=603) were not included in this analysis

4.4.2 Fixed effects on neonatal behaviour scores

Table 4.3.a shows the relationships between litter size at birth and the neonatal traits. Lambs from smaller litters had higher birth weights that those from larger litters (F test =111; P<0.001). Litter size affected whether a lamb was Assisted or not (Likelihood ratio χ^2 = 92.44; P<0.001), with twin lambs requiring lower levels of BA than either singles or triplets (F test = 8.19; P<0.001). There was no over-all relationship between litter size at birth and either LV or SA in this dataset.

Table 4.3.b shows the relationship between sex of the lamb and the neonatal traits. Only birth weight differed significantly between the sexes with males heavier than females (F test = 8.59; P = 0.003). There were no differences in whether or not lambs were Assisted at birth (Likelihood ratio χ^2 = 2.01; P>0.1), nor in the amount of BA or SA given. There was a trend for male lambs to be less vigorous (i.e. have higher scores) at 5 min after birth than females (F test = 3.26; P = 0.071).

Lambs born to 2 year old ewes (usually first parity) weighed less at birth than lambs from older (multiparous) ewes (F test = 3.93; P<0.001). Lambs which needed less BA had lower (i.e. better) LV scores (Fig. 1a; F test = 11.71, P<0.001). Regarding the relationship between BA and SA, overall, BA score was a significant contributing factor for the amount of SA needed (Fig 1b: F test = 2.59, P = 0.036), however, pairwise comparisons between each BA category indicate that this difference is mainly caused by the high value of BA category 4. Lambs which had lower (i.e. better) LV scores needed less SA than lambs with higher LV scores (Fig. 1c; F test = 18.87, P<0.001).

Table 4.3. Mean (± standard error) for all traits measured at birth for litter size (a) and lamb sex (b)[1]. Maximum Likelihood Ratio χ² for whether a lamb needed assistance (1) or not (0) at birth. Values are given as actual observations (expected observations).

(a) Trait		**N**	**Assisted or not**		**Birth weight**	**Birth assistance**	**Lamb vigour**	**Sucking assistance**
			0	**1**				
Litter size	1	297	66 (128.2)	231 (168.8)	5.71 ^{c} ± 0.14	1.38 ^{a} ± 0.20	1.63 ± 0.15	1.46 ^{a} ± 0.16
	2	410	235 (177.0)	175 (233.0)	4.72 ^{b} ± 0.14	0.93 ^{b} ± 0.18	1.71 ± 0.14	1.56 ^{a} ± 0.15
	3	88	41 (38.0)	47 (50.0)	3.97 ^{a} ± 0.16	1.36 ^{a} ± 0.22	1.71 ± 0.16	1.75 ^{b} ± 0.17
	4	4	3 (1.7)	1 (2.3)	4.11 ^{ab} ± 0.40	0.58 ^{ab} ± 0.54	1.05 ± 0.38	1.45 ^{ab} ± 0.37
P			***		***	***	NS	†

(b) Trait		**N**	**Assisted or not**		**Birth weight**	**Birth assistance**	**Lamb vigour**	**Sucking assistance**
			0	**1**				
Lamb sex	Male	368	-	-	4.71 ± 0.17	1.13 ± 0.22	1.54 ± 0.16	1.55 ± 0.17
	female	431	-	-	4.54 ± 0.17	1.00 ± 0.22	1.43 ± 0.16	1.56 ± 0.17
P					**	NS	†	NS

†*P* < 0.10, **P* ≤0.05, ***P* ≤ 0.01, ****P* ≤ 0.001
[1] Means within a column sharing a common superscript are not significantly different (*P* > 0.05)

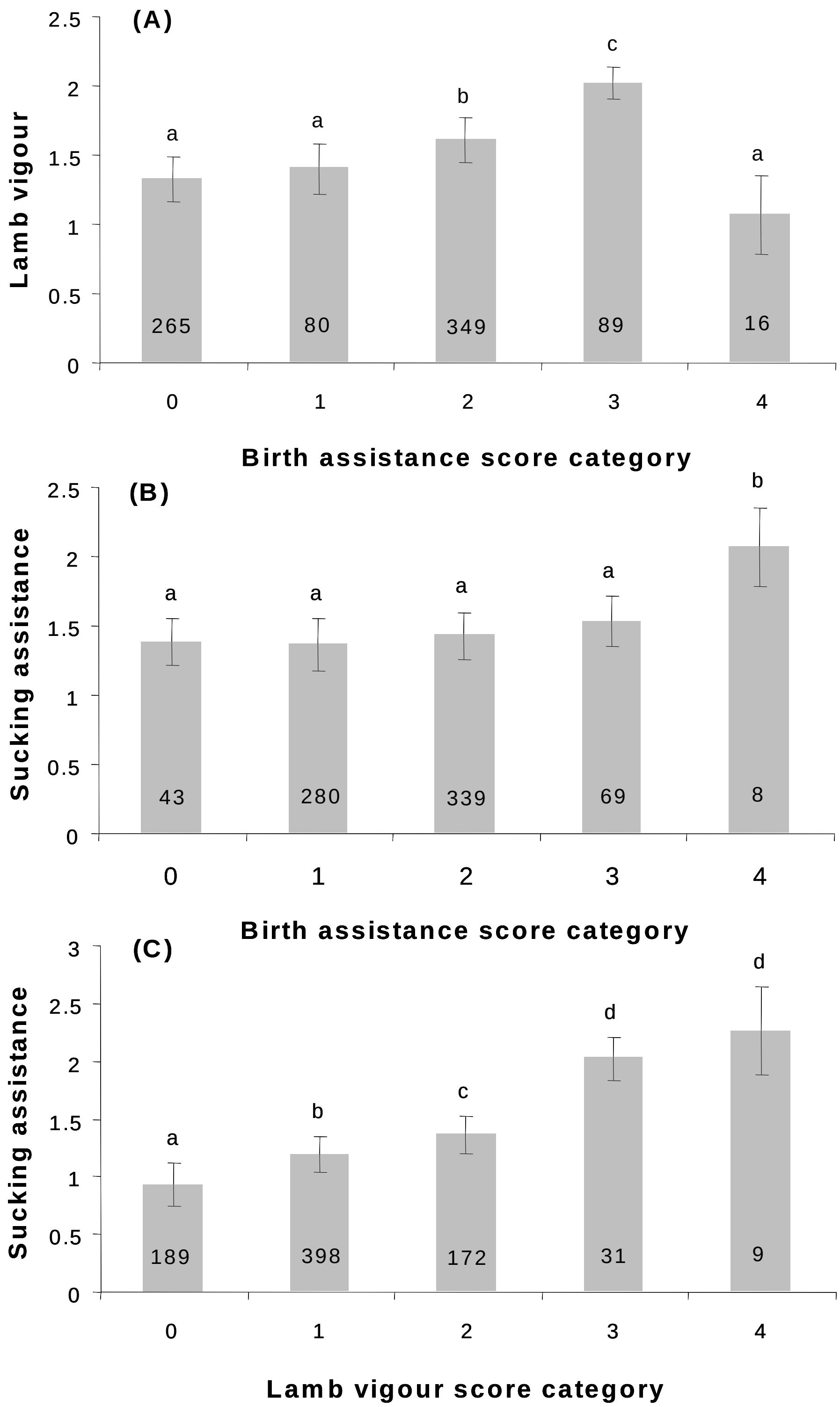


Figure 4.1. Relationships between neonatal scores (mean ± s.e.): birth assistance and lamb vigour **(A)**; birth assistance and sucking assistance **(B)**; and, lamb vigour and sucking assistance **(C)**. Columns indicate the number of lambs in each score category. Means sharing a common character in their superscript do not differ significantly (*P*>0.05).

4.4.3 Genetic parameters

Table 4.4 shows the genetic parameters estimated for BA, LV and SA. For BA, direct additive genetic effects and the permanent environmental effect of the litter explained approximately equal proportions of the phenotypic variance. In contrast, for LV and SA, the permanent environmental effect of the litter explained a greater proportion of the phenotypic variance than direct additive genetic effects. Heritabilities for BA and SA were moderate (BA, 0.43 ± 0.063; SA, 0.27 ± 0.045), while the heritability for LV was lower (0.15 ± 0.059). The genetic correlation between BA and LV was low-moderate and negative (-0.29 ± 0.198) but that between BA and SA was high and positive (0.81 ± 0.136). The genetic correlation between LV and SA was low-moderate and negative (-0.25 ± 0.202). However, the large standard errors of the genetic correlations suggest that they are not significantly different from zero.

Table 4.4. Estimates of phenotypic variance (V_p), genetic variance (V_g), ratio of permanent environmental effect of the litter variance to phenotypic variance (σ_{pe}^2), and heritabilities (in bold on diagonal), phenotypic correlations (above diagonal) and genetic correlations (below diagonal) for birth assistance, lamb vigour and sucking assistance scores in Texel sheep[1]

	BA	**LV**	**SA**
V_p	0.851 ± 0.049	0.558 ± 0.033	0.642 ± 0.036
V_g	0.367 ± 0.064	0.084 ± 0.035	0.176 ± 0.031
σ_{pe}^2	0.256 ± 0.052	0.304 ± 0.037	0.369 ± 0.039
BA	**0.43** ± 0.063	0.17 ± 0.040	0.21 ± 0.037
LV	-0.29 ± 0.198	**0.15** ± 0.059	0.26 ± 0.038
SA	0.81 ± 0.136	-0.25 ± 0.202	**0.27** ± 0.045

[1] All standard errors (± s.e) are given from a 3-variate model

4.5 Discussion

4.5.1 TM-QTL Genotype

Our results indicate that the TM-QTL genotype has a significant influence on the sucking ability of lambs (SA scores). TM-QTL has an interesting mode of inheritance, exhibiting a polar overdominant mode of inheritance for loin traits, with paternally expressed imprinting (MACFARLANE *et al.* 2010a). This type of inheritance results in an increased effect in the loin area only when the QTL is inherited from the sire ($TM^S/+^D$) but has no effect if the QTL is inherited from the dam (either $+^S/TM^D$ or TM^S/TM^D). In this study, we found that lambs which inherited a copy from the sire or dam (both $TM^S/+^D$, TM^S/TM^D and $+^S/TM^D$) had significantly higher SA scores (indicating a reduced sucking ability) than homozygous non-carrier lambs ($+^S/+^D$). Although there was no significant difference found between $+^S/TM^D$ and $+^S/+^D$, the relatively low number of animals in this class make this effect questionable. All the TM-QTL containing genotypes have higher SA and are very similar in value. The significant interaction found between TM-QTL genotype and birth weight in the SA analysis arises because $+^S/TM^D$ lambs weighed less at birth than either $TM^S/+^D$ and TM^S/TM^D lambs, although, again, this effect may be due to the low numbers of animals with the $+^S/TM^D$ genotype and needs to be validated in future studies.

Lambs which inherit the QTL from the sire may weigh slightly more at birth but they also have a tendency to require more assistance at birth, as well as having poorer sucking ability, resulting in implications regarding utilisation of this genotype within breeding programmes. For example, an investigation of lambs expressing the *callipyge* gene found no effect on birth weight or shape in the lambs and no increase in birth difficulty in ewes giving birth to carrier lambs (JACKSON *et al.* 1997). However, expression of the *callipyge* gene results in muscle hypertrophy (CARPENTER *et al.* 1996) which largely occurs in the postnatal period, and neonatal lambs carrying the *callipyge* gene have normal muscle development at birth (JACKSON *et al.* 1997).

Although there was no effect of QTL on LV at 5 minutes after birth, the negative effect on sucking ability can have several implications for the lamb. Previously, we have shown that lamb sucking ability is associated with lamb survival (DWYER *et al.* 2001; DWYER and LAWRENCE 2005b). However, in this present study we were unable to fully investigate the effect of carrier status on lamb survival as tissue for genotyping was not collected until after the majority of the non-surviving lambs had died. However, he data suggests that any potential alteration in muscle contractility or fibre type proportion which may have occurred as a result of expressing the QTL may affect lamb functional behaviour. This may place lambs which are slow to suck at a disadvantage; energy intake is reduced, resulting in a greater loss of energy reserves (Nowak and Poindron 2006), and insufficient uptake of immunoglobulin impairs the developing immune system (SAWYER *et al.* 1977). Lambs with poor sucking ability may also have impaired mother-young bonding. Development of mother preference is mostly dependent on the first successful sucking bouts (NOWAK *et al.* 1997; NOWAK and POINDRON 2006) and is the earliest indicator of postnatal learning (VINCE 1993; VAL-LAILLET *et al.* 2009). The inability to suck during the first few hours after birth reduces lambs' ability to discriminate its mother, an effect that cannot be attributed to reduced colostrum intake (NOWAK *et al.* 1997; VAL-LAILLET *et al.* 2004). A reduction in sucking events during early lactation, due to inadequate mother-young bonding, may also result in a drop-off in milk production in the ewe (MARNET and MCKUSICK 2000; CIMEN and KARAALP 2009).

4.5.2 Fixed effects

The litter size that a lamb is born into has effects on many neonatal traits. Single lambs weigh more at birth than lambs from multiple litters (twins, triplets and quads) and needed more assistance at birth (OWENS *et al.* 1985; DWYER 2003). As expected, male lambs were significantly heavier than females; however, there was a tendency for females to be more vigorous after birth. Previous studies have shown that birth weight affects vigour after birth (DWYER 2003), which may account for the sex difference in lamb vigour; however, birth weight is added as a covariate in the model used to calculate lamb vigour. Thus the results obtained are essentially independent of linear effects of lamb birth weight, suggesting that non-linear effects of birth weight or other factors, such as skeletal conformation, may also account for the sex difference observed for lamb vigour (SMITH 1977). It was unexpected that lamb sex had no effect on birth assistance score as other studies have shown that dystocia is affected by lamb sex (with males requiring more assistance), even when controlled for birth weight (NAWAZ and MEYER 1992). The effects of sex on sucking ability appear to vary between studies, with some studies reporting sex differences (DWYER 2003) and others not (WASSMUTH *et al.* 2001).

4.5.3 Genetic parameters

All neonatal genetic analyses were conducted on the full data set of 799 lambs; all lambs had a complete set of neonatal records – BA, LV, SA and birth weight. For all neonatal traits, the permanent environmental effect of the litter amounts to between 30-57% of the phenotypic variance, while direct additive genetic affects amounts to between 15-43% of the phenotypic variance (Table 4.4). The broad range of variance found in the permanent environmental effect of the litter may be due to the fact that litter variance includes both direct maternal variance and the environmental effect of the uterine environment, such as competition-related differences of litter size in *utero* (BRADFORD 1972), pelvic dimensions of the ewe (FOGARTY and THOMPSON 1974; HAUGHEY *et al.* 1985) or in the ability of ewes to provide nutrition to her lambs (DESAI and HALES 1997).

There are currently few estimates of genetic parameters available in the literature for neonatal traits in lambs. Nonetheless, in this study, the heritability for birth assistance (0.43) is comparable with the estimated heritability of morphological growth traits in wild populations (0.46; MOUSSEAU and ROFF 1987) and to various growth traits, such as birth weight, weight at weaning and mature weight (0.18 to 0.50, MARÍA *et al.* 1993; 0.15 to 0.41, SAFARI *et al.* 2005). These are higher estimates than that suggested by SMITH (1977), which reported a heritability for dystocia of 0.13 ± 0.03. Other studies have looked at ease of birth by recording the length of parturition (defined as the first definite sign of impending parturition until the birth of a specific lamb), inferring that more difficult births will take longer. These studies suggest heritabilities for length of parturition between 0.03 ± 0.04 to 0.05 ± 0.03 (CLOETE *et* *al.* 2002; CLOETE *et al.* 2006). The SMITH (1977) study has only level of assistance categories (1 – no assistance, 2 – required assistance, 3 – very difficult, 4 – caesarean or ewe died as a result of dystocia) but no temporal aspect. CLOETE *et al.* (2002) and (2006) studies only recorded the length of parturition but did not include any estimation of the amount of assistance required at birth. Therefore, the inclusion of both of these aspects in the birth assistance scores as described in MATHESON *et al*. (2011) are a more complete method for selection using levels of birth assistance and for estimating heritability. Thus, better measurement of a trait, in and of itself, generates higher heritability, however, the presence of measurable heritability is strong evidence that genes are involved (JOHNSON *et al.* 2011).

In this present study, the heritability of lamb vigour is estimated at 0.15 ± 0.06, which is similar to that reported by SMITH (1977), where lamb vigour was estimated at 0.1 ± 0.03, although, for the SMITH (1977) study, analytical purposes lambs were scored as vigorous and not vigorous (0/1). For the scores developed in MATHESON *et al*. (2011), the ranges of scores were carefully selected to be representative of the underlying biology of lamb behaviour (scores ranging from 0-4). There are estimates of heritability using the latency from birth to specific behaviours: latency from birth to standing, ranging from 0.10 ± 0.05 and 0.12 ± 0.05 (Marino and Dormer respectively, CLOETE *et al.* 2002) to 0.23 ± 0.06 (Marino, CLOETE *et al.* 2006); and latency from birth to sucking, ranging from 0.08 ± 0.05 and 0.07 ± 0.04 (Marino, CLOETE *et al.* 2002; CLOETE *et al.* 2006, respectively) to 0.12 ± 0.06 (Dormer, CLOETE *et al.* 2002). However, latency data is difficult to collect in large quantities on farm, and given a sucking score, a combination of both latency and level of assistance, heritability of 0.27 is suggestive that score data may be an easier method of data collection. Interestingly, the heritabilities of the neonatal traits are similar to the range estimated for survival in Scottish Blackface lambs (0.18-0.33; SAWALHA *et al.* 2007).

In this study, all neonatal traits were analysed as lamb traits, even though BA and SA are composite traits, having components of ewe and lamb behaviour as well as levels of human intervention. Thus, some aspects of maternal behaviour are accounted for within the additive genetic variance, such as sucking co-operation and absence of aggression towards the neonate (ALEXANDER *et al.* 1988).

As previously mentioned, inheritance of the TM-QTL genotype, with the associated negative effect on sucking ability, may have implications for its use in breeding programmes. Nonetheless, this negative effect may be opposed by selection for improved neonatal traits due to the high genetic variance present in these traits. In general, selection experiments based on quantitative behavioural traits are few and should be the focus of future studies (KINGSOLVER *et al.* 2001). Further work is needed to determine whether selection for improved neonatal lamb fitness or behaviour traits negatively correlates with performance traits in later life.

4.6 Conclusion

Possession of one or two copies of TM-QTL increases the amount of required sucking assistance. These effects may influence the acceptability of the QTL in commercial production. However, the heritability of all the measured neonatal traits suggests that there is sufficient variation available within the population to account for the negative effects of TM-QTL, thus allowing the inclusion of TM-QTL in breeding programmes by selecting for improvement in neonatal traits.

CHAPTER FIVE

GENETIC PARAMETERS FOR FITNESS AND NEONATAL BEHAVIOR TRAITS IN SUFFOLK SHEEP

5.1 Abstract

Two main causes of lamb mortality are dystocia and low neonatal vigor. Both require high levels of human intervention to ensure survival of the lambs. Therefore, selection for traits requiring lower levels of input is desirable. This study investigated whether the welfare of neonatal lambs could be improved through selection of parents with superior vigor characteristics. Neonatal data were collected over two years from 290 flocks belonging to the UK Suffolk Sheep Society. Each lamb was scored on: birth assistance (BA), scores range from 0–4, where 0= unassisted and 4= veterinary assistance required; lamb vigor at 5 minutes of age (LV), where 0= lamb standing and 4= lamb unable to lift head; and sucking assistance (SA), where 0= sucking without assistance and 4= lamb helped to suck when more than 3 days old.

Genetic parameters were estimated using ASREML, with the variance components of univariate models used to estimate heritabilities. Heritabilities were moderate for BA (0.26, s.e. 0.03), LV (0.40, s.e. 0.04) and SA (0.32, s.e. 0.03), with genetic correlations between neonatal traits all moderate to high and positive. These results show that neonatal lamb behavior has a moderate heritability, comparable to those of typical production traits. The analysis also shows that neonatal survival traits of birth assistance and sucking assistance are moderately heritable when treated as a lamb trait, rather than a sire or ewe trait, indicating the selection should target the lambs in order to successfully, and efficiently, improve survival.

5.2 Introduction

Neonatal lamb behaviors are important indicators for survival. Worldwide estimates suggest that 15-30% of lambs die before weaning, with mortality rates highest within the first 3 days of postnatal life (NOWAK *et al.* 2000; SAWALHA *et al.* 2007; BRIEN *et al.* 2010). Lamb survival is, to a degree, dependent upon an easy delivery and the expression of appropriate behaviors from both mother and offspring. Neonatal lambs have well-adapted behavior patterns expressed immediately after birth (NOWAK and POINDRON 2006), and need to be vigorous in order to rapidly find the udder and suck.

Studies have reported breed differences in the latency from birth to standing (SLEE and SPRINGBETT 1986; DWYER *et al.* 1996) and line differences in the latency from standing to sucking, suggesting that the rate at which a lamb stands and sucks may be affected by gene action (CLOETE and SCHOLTZ 1998; DWYER *et al.* 2001). Therefore, since line and breed differences are found, and selection for lamb survival has been successful (KNIGHT *et al.* 1988; KILGOUR and HAUGHEY 1993; CLOETE and SCHOLTZ 1998), it would suggest that there is a genetic basis to lambing difficulty and lamb vigor (ALEXANDER *et al.* 1990c; CLOETE and SCHOLTZ 1998; DWYER *et al.* 2001; CLOETE *et al.* 2002; DWYER and LAWRENCE 2005a). However, genetic parameter estimates for behavioral traits contributing to lamb survival are scarce (HOHENBOKEN 1985; HINCH 1997; MACFARLANE *et al.* 2010b).

Terminal-sire sheep breeds are genetically selected for high lean growth and other carcass [or morphological] traits (AMER *et al.* 2007; BYRNE *et al.* 2010) and, in addition, on extremes of conformation and bone (RIUS-VILARRASA *et al.* 2010). A study by SMITH (1977) states that artificial selection for production traits, growth rate and mature size, may be carried out with no consideration required for dystocia and lamb vigor, due to their low heritabilities, 0.13 and 0.1, respectively. However, selection for increased weight and growth rate may have resulted in an increase in dystocia at birth (GROMMERS *et al.* 1985; DWYER and BUNGER in press). Indeed, BOMAN (2011) warns that selection for specific traits may constitute an unpredictable risk of unwanted side-effects and a subsequent risk of substantial loss of genetic variation. This suggests that neonatal fitness/behavior and welfare traits should be included within breeding programs, which are based mostly on growth and carcass traits (MACFARLANE *et al.* 2010b). Widening breeding goals by including fitness and welfare traits into breeding indexes may result in a more balanced breeding program and greater profitability than selection on production traits alone (LAWRENCE *et al.* 2004).

However, one of the issues surrounding the inclusion of fitness traits in breeding programs is that literature suggests life history traits have lower heritability than morphological and growth traits (FISHER 1930; MOUSSEAU and ROFF 1987; FALCONER and MACKAY 1996). Complex behavioral characters and life history traits integrate both morphological and physiological characters within a single life stage, e.g. survival shortly after birth may depend upon body shape and size during birth as well as the physiological processes involved with standing and sucking (HENDERSON 1990; STIRLING *et al.* 2001). This amalgamation of traits led PRICE and SCHLUTER (1991) to suggest that life history traits have a lower heritability because they are one step further down the causal pathway from genes to phenotype, with additional random factors coming into play at each step.

Genetic solutions have the potential to, cumulatively and sustainably, improve the fitness traits of birth assistance and lamb behavior, but larger data sets are needed to estimate initial genetic parameters in order to optimize the integration of these data into breeding programs. However, reproductive and behavioral traits relating to development are difficult to measure on farm. In order to achieve this objective, simple, proxy methods (scoring systems) have been developed to assess the level of birth difficulties and lamb vigor on farm enabling ‘mass phenotyping’ (MATHESON *et al.* 2011). For the development of these scores, detailed data on parturition and latency from birth to key behaviors (such as standing, seeking the udder and sucking successfully) were recorded. This resulted in three scoring systems, for birth assistance, lamb vigor and sucking assistance, with a broad range of categories within each scoring system. Lamb vigor is purely a lamb fitness trait, whereas the birth assistance and sucking assistance systems contain management decisions, such as manual assistance, in their scores.

Therefore, the objective of this study was to estimate the heritability of neonatal lamb fitness traits and to evaluate the genetic (co)variances between neonatal traits and the (co)variances between neonatal and subsequent production traits. This study, therefore, also provides the opportunity to determine whether lambs with better neonatal behavior scores had improved production/performance in later life (up to 20 weeks).

5.3 Materials and Methods

5.3.1 Animals

Data were collected in the years 2008 and 2009 from 290 flocks belonging to the Suffolk Sheep Society, UK. A total of 11,092 lambs with complete neonatal records were extracted from the BASCO data base. BASCO data Ltd is an industry-generated database providing the UK sheep and beef livestock sector with a platform for pedigree and performance recording (http://www.basco.org/). Lambs in this database have been recorded for performance traits, on which genetic evaluations are eventually based, including -: live weight at 8 weeks, and live weight, ultrasound muscle depth and ultrasound fat depth at 20 weeks. For financial reasons, flock owners tend to enter only the performance records of their 'best' animals into the database.

5.3.2 Data collection

Scoring systems, based on lamb behavioral development, have previously been developed for birth assistance, lamb vigor and sucking assistance (Table 5.1; MATHESON *et al.* 2011) and were used here. Each lamb was scored on birth assistance (BA), lamb vigor (LV, at 5 minutes of age) and sucking assistance (SA).

Neonatal scores and birth weight of the lamb were recorded by flock owners at birth, with comprehensive guidelines to the scoring systems given to each flock owner to minimize the subjectivity of the scores. In addition, for a sub-set of lambs selected by the flock-owners, live weight at approximately 8 weeks of age (W8WT), live weight at approximately 20 weeks of age (W20WT) as well as ultrasound muscle depth (UMD) and ultrasound fat depth (UFD) at 20 weeks were recorded. W8WT and W20WT were recorded by the flock owner with UMD and UFD measured by technicians trained in ultrasound techniques that travel to each flock.

Table 5.1 Definitions of birth assistance scores, lamb vigour scores and sucking assistance scores

(1)	**Birth assistance scores**
0	Unassisted or easy uncomplicated delivery of short duration (<30 minutes)
1	Unassisted or easy uncomplicated delivery of longer duration (>30 minutes)
2	Minor assistance required. Presentation corrected, little effort needed to deliver lamb
3	Major assistance required. Difficult delivery needing effort to deliver lamb
4	Veterinary assistance required
(2)	**Lamb vigour scores** (at 5 minutes of age)
0	Extremely active and vigorous lamb, has been standing on all 4 feet
1	Very active and vigorous lamb, standing on back legs and on knees
2	Active and vigorous lamb, on chest and holding head up
3	Weak lamb, lying flat, able to hold head up
4	Very weak lamb, unable to lift head, little movement
(3)	**Sucking assistance scores**
0	Lamb sucking well without assistance within 1 hour
1	Lamb sucking well without assistance within 2 hours
2	Lamb given sucking assistance/ fed by stomach tube once or twice in first 24 hours after birth
3	Lamb given sucking assistance, fed by stomach tube more than twice, needing help after 1 day old, but able to suck by 3 days old
4	Lamb still needing help to suck when more than 3 days old

5.3.3 Statistical analysis

The association between the neonatal traits and whether or not a lamb is performance recorded after birth was analyzed using ANOVA (Genstat version 11.1.0.154, 2008), with whether an animal had neonatal scores recorded at birth only, neonatal + 8-weeks or neonatal + 8-weeks + 20-weeks fitted as a factor. All genetic parameters, genetic correlations and phenotypic correlations were obtained by linear mixed animal models using ASReml (GILMOUR *et al.* 2006). Parameters and correlations for the neonatal traits only (BA, LV and SA) were obtained using a 3-variate model containing 11,092 records. Parameters and correlations for the performance traits only (W8WT, SWT, UMD and UFD) were obtained using a 4-variate model containing 2,885 records. Genetic and phenotypic correlations between the 3 neonatal traits and the 4 performance traits were obtained by means of a 7-variate model containing 2,885 records. The pedigree structures for both datasets (11,092 animals and 2,885 animals) are shown in Table 5.2.

Table 5.2 Pedigree structure for neonatal traits (total number of animals in pedigree = 28,112) and performance traits (total number of animals in pedigree = 8,485)

Dataset	Records	Sires[1]	Dams[1]	Litters	FYG[2]
Neonatal	11092	588	5595	6889	290
Performance	2885	178	1776	2136	76

[1] number of sires or dams with offspring with records; [2] number of flock-year-management groupings

Fixed effects used for the neonatal traits and performance traits models were: flock-year management group (290 levels), age of dam (14 levels), season of birth (2 levels; season 1 – lambs born December to February, season 2 – lambs born March to June), litter size (5 levels), lamb sex (2 levels) and a linear covariate of birth weight. For the performance trait 4-variate model, fixed effects of BA, LV and SA were added to the model, to elucidate the relationship between neonatal traits and performance traits. Random effects for both models were the direct additive (animal) effect and the environmental effect of the litter, along with the residual. The environmental effect of the litter was used to account for some dams producing more than one lamb in one year. However, the pedigree structure was such that it was not possible to separate maternal additive effects, maternal permanent environmental effects and temporary environmental effects for any of the traits.

In this study, data were not transformed before analysis given that heritabilities are scale invariant and remain unchanged when scale transformations are applied (BRYANT 1986). Although there are statistically more rigorous mathematical algorithms based upon assumptions of ordered categories and concepts of thresholds (GIANOLA and FOULLEY 1983; HARVILLE and MEE 1984), these have been compared with 'incorrect' linear animal models and both show good agreement (PURVIS and HILLARD 1997). Indeed, JORGENSEN (1994) suggests that best linear unbiased prediction (BLUP) should not be replaced by non-linear algorithms until they can be performed with an animal model.

5.4 Results and Discussion

5.4.1 Neonatal traits and performance recording

Results of the ANOVA showed that neonatal fitness and behavior traits had significant effects on the probability of later performance recording of these lambs. Lambs which only had neonatal records (i.e. were not selected for further performance recording) had higher BA (i.e. required more assistance at delivery), higher LV (i.e. were slower to stand) and higher SA scores (i.e. required more assistance to suck) when compared with lambs that had neonatal + 8-week records (Table 5.3). Similarly, lambs that had neonatal + 8-week records only had higher BA, LV and SA scores when compared with lambs that had neonatal + 8 + 20-week records (Table 5.3). Therefore, lambs that had higher neonatal scores were less likely to be performance-recorded in later life (20 weeks of age), while lambs that had easier births and those who were more vigorous, i.e. stood quickly and sucked soon after birth, continued to be recorded in later life. This indicates that neonatal scores are a good predictor of the probability of future performance recording, and emphasizes that the performance data are censored records.

Table 5.3 Mean neonatal scores for lambs having neonatal records only, records at birth and 8 weeks of age and recorded at birth through to 20 weeks of age. Means (± s.e.) were calculated using ANOVA. Within a row, means without a common superscript differ (P < 0.05).

Trait	Neonatal only	Neonatal + 8 weeks	Neonatal + 8 + 20 weeks	Variance Ratio	*P*
N	5426	2761	2905		
Birth assistance	$2.49^{a} \pm 0.01$	$2.38^{b} \pm 0.02$	$2.21^{c} \pm 0.02$	85.99	***
Lamb vigour	$2.26^{a} \pm 0.01$	$2.20^{b} \pm 0.02$	$1.92^{c} \pm 0.02$	156.76	***
Sucking assistance	$2.29^{a} \pm 0.01$	$2.23^{b} \pm 0.02$	$1.92^{c} \pm 0.02$	167.85	***

†P < 0.10, *P < 0.05, ***P < 0.001.

Of the lambs that were not recorded past birth, some will have died and some will have been considered to be of insufficient quality to be performance recorded. Pre-weaning survival is affected by both parturition and neonatal adaptation to post-natal life (MELLOR and STAFFORD 2003), with a positive correlation between rapid neonatal progress and lamb survival (OWENS *et al.* 1985; DWYER *et al.* 2001). Slow behavioral progression may have several consequences: lambs slow to stand and suck are at risk of depleting their energy reserves (NOWAK and POINDRON 2006), developing hypothermia (GROMMERS *et al.* 1985; DWYER and MORGAN 2006; POLLARD 2006), they may have a reduced absorption of immunoglobulins (NOWAK and POINDRON 2006) and may have impaired mother-young bonding (NOWAK *et al.* 1997; DWYER *et al.* 2003; NOWAK and POINDRON 2006; NOWAK *et al.* 2007), resulting in poor maternal care and early lamb death (NOWAK 1996).

Post hoc pair-wise comparisons of the data show that the probability of being performance recorded in later life was affected by all three of the neonatal traits (BA, LV and SA). This was in contrast to MACFARLANE *et al.* (2010b), who found that BA had no effect on the probability of being performance recorded. This was attributed, in that study, to the fact that most pure-bred Suffolk ewes lamb indoors and have a high level of assistance available, which may prevent and reduce trauma (see also, NAWAZ and MEYER 1992; BINNS *et al.* 2002). However, ewes were managed similarly in the present study, which did show an effect of BA. The present study involved a larger number of animals, with MACFARLANE *et al.* (2010b) having approximately 10% of the records used in this study, which may have increased the chances of finding a significant relationship between BA score and performance recording. Another factor may have been that the scoring system used in this study was designed as a 5-point scale, allowing an approximately normal distribution of the data. This resulted in a system sufficiently refined to identify variation in lambs, particularly at the ‘good end’ of the scale, thus increasing the range of selection possibilities.

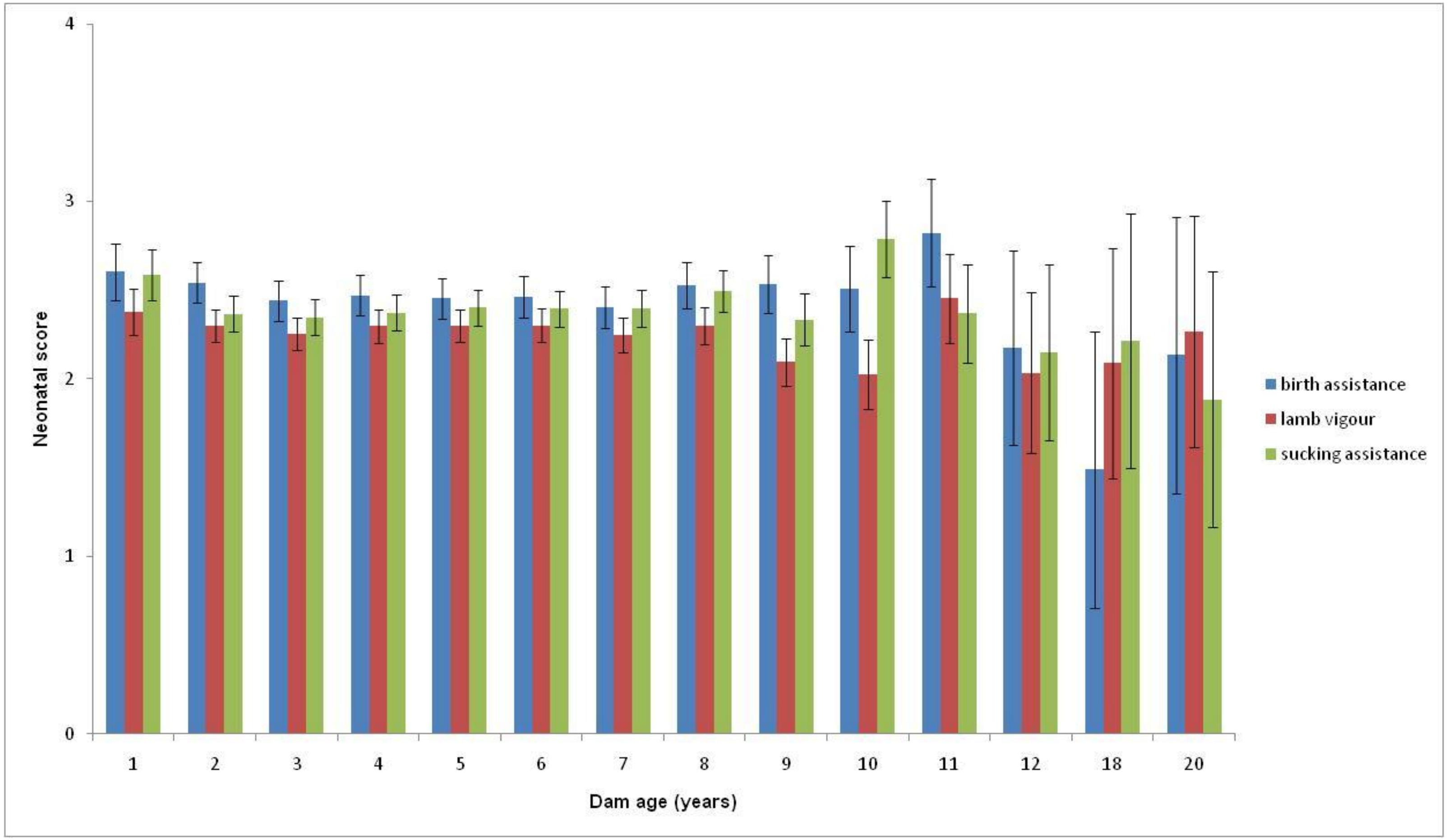
5.4.2 Fixed effects on neonatal and production traits

For the ASREML analysis, although flock-year management group was a significant source of variation for all traits (both neonatal and production), the results are not presented. Year of birth and flock ID (which includes both geographical and livestock management differences) are not repeatable and are therefore of limited interest.

5.4.2.1 Dam age

Overall, lambs with older dams had lower BA score, i.e. they required less assistance at birth than younger dams; however, they had higher SA scores, requiring more sucking assistance (figure 5.1). There was no effect of dam age on LV score. Lambs with older dams were slightly heavier at 8 weeks than offspring of younger dams, although there was no effect of dam age on live weight at 20 weeks, which is expected, as maternal effects usually decrease with lamb age. There was no effect of dam age on either muscle or fat depth at 20 weeks.

Figure III.I. Relationship between the neonatal scores (birth assistance, lamb vigour and age of dam (years), excluding the covariate of birth weight. Predicted mean ± s.e. for the neonatal scores are from 11092 animals.



Dam age, and by consequence parity, is a major factor in neonatal traits. First parity, younger, ewes generally have higher rates of dystocia than more mature and experienced ewes (SMITH 1977; DAWSON and CARSON 2002; DWYER and LAWRENCE 2005a). In general, first parity ewes show more disturbed behaviors resulting in lambs which are slower to stand and suck than lambs born to older and more experienced ewes (DWYER 2003; DWYER *et al.* 2005). However, this is in contrast with the findings in this study, where lambs from older dams are slower to suck, although it is not known if there are any udder-related or reduced milk problems in these ewes, which may result in an increase in sucking assistance, although the growth rate from birth to 8 weeks of age may argues against this. Dam age is reported to affect early growth rate, where lambs from younger ewes have slower growth rates (PEETERS *et al.* 1996; DAWSON and CARSON 2002; AFOLAYAN *et al.* 2007). Although, similar to the results reported in this study, PEETERS *et al.* (1996) found that after 16 weeks of age, lambs from younger ewes are not significantly lighter than those from older ewes. The literature for effects of dam age on lamb muscle and fat depths is inconclusive, with GREEFF *et al.* (2008) reporting no effects, while AFOLAYAN *et al.* (2007) report no effects on muscle depth but an increase in fat depth with a corresponding increase in dam age.

5.4.2.2 Season of birth

There was no effect of season of birth on the amount of birth or sucking assistance a lamb required. However, lambs which were born in season 2 (that is later in the lambing period) were more vigorous than those from season 1 (Table 5.4.1). There was no effect of season of birth on live weight at 8 weeks of age. However, lambs that were born in season 1 weighed more at 20 weeks, had greater depth of muscle and had more fat on top of the muscle when compared with lambs from season 2 (Table 5.4.2).

Table 5.4 Relationship between season of birth and (1) neonatal scores (birth assistance, lamb vigour and sucking assistance), (2) performance traits (8 week weight, 20 week weight, ultrasound muscle depth and ultrasound fat depth). Lambs from season 1 were born between Dec-Feb; lambs from season 2 were born between Mar-June. Predicted mean ± s.e. for (1) neonatal scores are from 11092 animals; predicted means for (2) performance traits are from 2285 animals.

Trait		Season 1	Season 2	*P*
(1)	N	9530	1562	
Birth assistance		2.42 ± 0.14	2.37 ± 0.15	†
Lamb vigour		2.28 ± 0.12	2.19 ± 0.12	***
Sucking assistance		2.38 ± 0.13	2.35 ± 0.14	†
(2)	N	2258	627	
8 week weight (kg)		24.67 ± 1.00	24.40 ± 1.04	†
20 week weight (kg)		52.71 ± 1.95	44.01 ± 2.03	***
Ultrasound muscle depth (mm)		30.04 ± 0.93	27.03 ± 0.97	***
Ultrasound fat depth (mm)		4.16 ± 0.41	3.01 ± 0.42	***

†$P < 0.10$, *$P < 0.05$, ***$P < 0.001$.

Although season of birth is a management decision, it is interesting to note the difference in lamb vigor between the seasons. Pure-bred Suffolks are usually mated to lamb between December and June, depending on the intended market for the lambs. Ram lambs intended for the ram lamb sales of the same year are usually born between December and the end of February, whereas ram lambs intended for the shearling (one-year old rams) sales of the following years are born later in the season (March to June). Ram lambs intended for the same-year sales are generally born as early as possible and selected for high birth weights and rapid growth in order to increase in size as much as possible before the sales. The aim is to have a ram lamb born at approximately 4kg that will reach a weight of approximately 100kg at 9 months of age. In contrast, ram lambs intended for the following year's sales may be selected for slower, more sustained growth. This is highlighted in the differences in the 20-week weight and muscle and fat depths. There may, in addition to any selection differences, be a difference in nutrition between the seasons. Lambs intended for the lamb sales may be fed higher quality forage, when indoors, and more concentrate than later-born lambs. In addition to any selection-based or nutritional differences, it is known that placental development differs between the seasons. For example, ewes mated in the summer, for winter-born lambs, have greater numbers of placentomes and a greater total placentome weight, and thus give birth to lambs of greater body weight, than ewes mated in the winter, for spring-born lambs (JENKINSON *et al.* 1995).

5.4.2.3 Litter size

Single lambs required more assistance at birth when compared with twins, even after adjustment for birth weight, but were not significantly different from triplets or quadruplets (Table 5.5.1). Singles and twins were more vigorous than triplets and quads; triplets, in turn, were more vigorous than quads. Singles and twins required less assistance to suck than either triplets or quads, and triplets required less assistance than quads. Single lambs had heavier weights at both 8 and 20 weeks and had more muscle depth (Table 5.5.2), while quads had less muscle depth than twins or triplets. Single lambs had greater fat depths than twins and triplets, but weren't significantly different from quads. There was no difference in fat depth between lambs from multiple litters.

Table 5.5 Effect of litter size on (1) neonatal scores (birth assistance, lamb vigour and sucking assistance) and (2) performance traits (8 week weight, 20 week weight, ultrasound muscle depth and ultrasound fat depth). Predicted mean ± s.e. for (1) neonatal scores are from 11092 animals; predicted means for (2) performance traits are from 2285 animals.[1]

	Litter size			
(1)	**1**	**2**	**3**	**4**
N	2546	7067	1419	55
Birth assistance	2.47 ± 0.10 [a]	2.40 ± 0.10 [b]	2.52 ± 0.10 [a]	2.50 ± 0.18 [ab]
Lamb vigour	2.23 ± 0.08 [a]	2.21 ± 0.08 [a]	2.31 ± 0.08 [b]	2.61 ± 0.15 [c]
Sucking assistance	2.27 ± 0.09 [a]	2.29 ± 0.09 [a]	2.43 ± 0.09 [b]	2.93 ± 0.16 [c]
(2)	**1**	**2**	**3**	**4**
N	734	1783	363	4
8 week weight (kg)	28.15 ± 0.53 [a]	25.91 ± 0.52 [b]	25.50 ± 0.56 [b]	24.45 ± 1.91 [b]
20 week weight (kg)	52.95 ± 1.04 [a]	51.02 ± 1.02 [b]	51.08 ± 1.09 [b]	43.38 ± 3.69 [c]
Ultrasound muscle depth (mm)	30.78 ± 0.50 [a]	30.32 ± 0.49 [b]	30.29 ± 0.52 [b]	29.15 ± 1.75 [c]
Ultrasound fat depth (mm)	4.18 ± 0.22 [a]	3.84 ± 0.21 [b]	3.87 ± 0.23 [b]	3.59 ± 0.77 [ab]

[1] Within a row, means sharing a common character in their superscript do not differ significantly ($P>0.05$).

Literature suggests that twins require less assistance than singles or other multiples during parturition (GROMMERS *et al.* 1985; DWYER 2003), in agreement with the current results. Single lambs and other multiples are often mal-presented, due to lack of space for maneuvering during parturition (FRASER and TERHUNE 1977; HINCH *et al.* 1986). Singles and twins are usually more vigorous and are quicker to suck, and thus need less assistance to suck, than other multiples (OWENS *et al.* 1985; CLOETE and SCHOLTZ 1998; DWYER 2003), possibly attributable to the lower birth weight of triplet and quadruplet lambs or placental insufficiency (MALLARD *et al.* 1998; REES *et al.* 1998). In keeping with other studies, this study found that single lambs had greater muscle and fat depths than twins or other multiples (BENNETT *et al.* 1991; AFOLAYAN *et al.* 2007). It is possible that this difference is due to the differing developmental stage of lambs at 20 weeks of age, with single lambs being more mature at a given age when compared with multiples. Fat and muscle deposition differ with stage of maturity, with growth nearer maturity laid down as fat with less bone and muscle than more immature growth (BENNETT *et al.* 1991).

5.4.2.4 Lamb sex

Males required more assistance at birth and were less vigorous than females, whereas there was no difference in the amount of sucking assistance required by sex (Table 5.6.1). Males were heavier than females at both 8 and 20 weeks and had more muscle depth (Table 5.6.2). There was no effect of sex on ultrasound fat depth.

Table 5.6 Effect of lamb sex on (1) neonatal scores (birth assistance, lamb vigour and sucking assistance) and (2) performance traits (8 week weight, 20 week weight, ultrasound muscle depth and ultrasound fat depth). Predicted mean ± s.e. for (1) neonatal scores are from 11092 animals; predicted means for (2) performance traits are from 2285 animals.

Trait		Sex		
		Male	**Female**	***P***
(1)	N	5490	5602	
Birth assistance		2.42 ± 0.14	2.38 ± 0.14	***
Lamb vigour		2.26 ± 0.12	2.22 ± 0.12	***
Sucking assistance		2.37 ± 0.13	2.36 ± 0.13	†
(2)	N	1485	1401	
8 week weight (kg)		25.41 ± 1.01	23.66 ± 1.01	***
20 week weight (kg)		51.91 ± 1.97	44.81 ± 1.97	***
Ultrasound muscle depth (mm)		28.89 ± 0.94	28.18 ± 0.94	***
Ultrasound fat depth (mm)		3.57 ± 0.41	3.61 ± 0.41	†

†$P < 0.10$, *$P < 0.05$, ***$P < 0.001$.

Studies have shown that dystocia is affected by lamb sex, with rates higher in males than females (SMITH 1977), even when controlled for birth weight (NAWAZ and MEYER 1992). Male lambs are often slower to go through behavioral progression, depending on the breed (DWYER 2003), although, the sex effect on lamb vigor may be confined to purebred lambs (SMITH 1977). Males are often skeletally larger and/or heavier at birth, increasing the risks of dystocia and mal-presentation, when compared with females (DWYER 2003). Difficulties during parturition may cause fetal hypoxia, slowing neural development (MALLARD *et al.* 1998; REES *et al.* 1998), or damage the central nervous system, thus impairing locomotive and sucking abilities of lambs (HAUGHEY 1980). The effects of sex on sucking ability appear to vary between studies, with some studies reporting sex differences (DWYER 2003; DWYER *et al.* 2005) and others not (WASSMUTH *et al.* 2001). As is consistent with literature, males have higher rates of post-natal growth than females (BENNETT *et al.* 1991; PEETERS *et al.* 1996; AFOLAYAN *et al.* 2007) and have more muscle (BENNETT *et al.* 1991), although there are no differences in fat depth (EVERITT and JURY 1966; BENNETT *et al.* 1991), suggesting a reduced proportion of fat in males, as expected.

5.4.2.5 Birth weight

In general, heavier lambs had more difficult births (regression coefficient ± s.e., 0.0877 ± 0.0065, P < 0.001), however, heavier lambs were also more vigorous (regression coefficient ± s.e., -0.0518 ± 0.0060, P < 0.001) and required less sucking assistance (regression coefficient ± s.e., -0.0865 ± 0.0064, P < 0.001). Lambs with heavier birth weights had heavier live weights at both 8 weeks and 20 weeks (regression coefficient ± s.e., 1.8375 ± 0.0527, P < 0.001, and, 1.8598 ± 0.1378, P < 0.001, respectively). In addition, heavier birth weight lambs had greater depth of muscle (regression coefficient ± s.e., 0.1974 ± 0.0571, P < 0.001), although there was no effect of birth weight on fat depth at 20 weeks (regression coefficient ± s.e., 0.0277 ± 0.0234, P > 0.1).

Birth weight is one of the fundamental factors influencing neonatal traits. Lambs which are heavier at birth are more likely to have problems at parturition (GROMMERS *et al.* 1985; OWENS *et al.* 1985; DWYER 2003), possibly due to an increased pectoral diameter of the shoulder-elbow flexion or to lack of space for turning within the uterine horn during parturition (DWYER *et al.* 1996). In general, heavier lambs are more vigorous that lighter lambs (OWENS *et al.* 1985), but both vigor and sucking ability may be adversely affected by increased birth weight (OWENS *et al.* 1985; DWYER *et al.* 2003), due to an increased risk of dystocia and mortality in larger lambs. In this study, birth weight was added as a covariate in the model used to calculate lamb vigor. As is consistent with literature, lambs with heavier birth weights had heavier live weights at both 8 weeks and 20 weeks, and thus had faster growth rates (GOOTWINE *et al.* 2006) and more muscle (GREENWOOD *et al.* 2000) than low birth weight lambs. However, recent studies into the correlation between birth weight and ultrasound fat depth in 20 week old Texel lambs showed no significant correlations (K. Moore, unpublished data).

5.4.3 Behavioral genetics

In a review paper of behavioral genetics, Faure (1994) suggests three reasons why the subject of behavioral genetics is less well studied. (1) Most behavior is perceived as being mainly environmentally determined, yet the genetic mechanisms inherent to behavior and performance traits are the same. (2) Behavior is perceived to be difficult to measure, however, the scoring system used in this study was developed for use on commercial farms, with the express purpose of improving the neonatal traits of birth assistance, lamb vigor and sucking assistance (MATHESON *et al.* 2011). These behavioral scoring systems have been shown to be indicative of the underlying behavioral responses, indicating their suitability for selection purposes. (3) Measures of behavioral traits are often not normally distributed, thus these scoring systems were designed as 5-point categorical scales, purposely allowing an approximately normal distribution of the data.

Literature suggests that traits closely associated with fitness generally have lower heritability than traits associated with morphology and growth (FISHER 1930; MOUSSEAU and ROFF 1987; FALCONER and MACKAY 1996), which are usually more performance/production related. Indeed, a study involving 7 sheep breeds (giving a single across-breed estimate) reported low heritabilities for neonatal fitness traits: dystocia and lamb vigor of 0.13 ± 0.03 and 0.10 ± 0.03, respectively (SMITH 1977). Higher values were reported by MOUSSEAU and ROFF (1987), who estimated a general heritability of mammalian fitness traits in wild populations and reported values around 0.26 ± 0.024. This disparity could be caused by many factors, e.g. different breeds/populations and/or scoring systems.

5.4.3.1 Neonatal genetic parameters

All neonatal genetic analyses were conducted on the full data set of 11,092 lambs; all lambs had a complete set of neonatal records – BA, LV, SA and birth weight. For all neonatal traits, the permanent environmental effect of the litter amounted to between 50-63% of the phenotypic variance, while direct additive genetic affects amounted to between 25-38% of the phenotypic variance (Table 5.7). The residual variance only amounted to between 11-20% of the phenotypic variance.

Table 5.7 Estimates of phenotypic variance (V_p), residual variance (V_r), genetic variance (V_g), permanent environmental effect of the litter variance (σ_{pe}^2), and heritabilities (in bold on diagonal), phenotypic correlations (above diagonal) and genetic correlations (below diagonal) for birth assistance, lamb vigour and sucking assistance scores in Suffolk sheep[1]

	Birth	Vigour	Sucking
V_p	0.626 ± 0.011	0.450 ± 0.008	0.539 ± 0.009
V_r	0.069 ± 0.011	0.050 ± 0.009	0.105 ± 0.011
V_g	0.159 ± 0.022	0.169 ± 0.018	0.162 ± 0.020
V_{pe}^2	0.398 ± 0.011	0.231 ± 0.007	0.272 ± 0.009
Birth	**0.26** ± 0.03	0.39 ± 0.01	0.29 ± 0.01
Vigour	0.68 ± 0.06	**0.40** ± 0.04	0.60 ± 0.01
Sucking	0.54 ± 0.07	0.80 ± 0.04	**0.32** ± 0.04

[1] All standard errors (± s.e.) are given from a 3-variate model

It would be expected at this early stage of life that the residual variance would account for less phenotypic variance than both additive genetic effects and litter effects. The only pre-natal effects the lamb encounters are its own genetics and the environment of the uterus in which it is growing (which itself has maternal factors as well as competition-related factors depending on pre-natal litter size). Prenatal maternal effects may be expected to be more important in sheep than cattle because of the greater relative variation in litter size in sheep, where litter size has consequences for pre- and postnatal growth and survival (BRADFORD 1972).

A large proportion of the phenotypic variation is attributable to the environmental effect of the litter. In cattle, the incidence of twins may range from 2.6% (MEE *et al.* 2011) to 4.5% (BELL and ROBERTS 2007). While, in sheep litter size can commonly range from singles to triplets and quadruplets (and occasionally more, although this is uncommon), lamb birth weight decreases as litter size increases, with estimates suggesting that twins are approximately 78% the weight of singles and triplets 62% of singles (DICKINSON *et al.* 1962). A study looking at the relationship between litter weight at birth and ewe weight at mating suggests that an increase in litter size increases the metabolic demand placed on the ewe, with estimates that single lambs were 22·6% and twin pairs 36·1% of the ewes' metabolic weight on average (DONALD and RUSSELL 1970). This is in contrast with cattle, where calf survival is maximised when the calf weight at birth is 7.2% of cow weight (JOHANSON and BERGER 2003). In this study, the environmental effects of the litter also includes maternal genetic effects (the genes carried by the ewe that affect maternal traits) as well as permanent environmental effects (environmental factors that affect the maternal input from the same ewe across different years), this effect must include aspects of maternal behavior, such as sucking cooperation and absence of aggression towards the neonate (ALEXANDER *et al.* 1988).

However, it must be noted that direct maternal effects could not be estimated due to the structure of the pedigree; therefore litter variance includes both direct maternal variance and the environmental effect of the uterine environment. The uterine environment is specific to each ewe and is not repeatable across years, dependent as it is on the ewe’s health and nutritional status and the number and sex of the lambs sharing the uterine environment. Indeed, MORRIS *et al.* (2000) and PURVIS and HILLARD (1997) reported that, at all lamb ages, the maternal permanent environment contributed more to the observed variation than the maternal genetic effect.

All heritabilities for neonatal traits were in the moderate range (Table 5.7); BA, 0.26 ± 0.03; LV, 0.40 ± 0.04; and SA, 0.32 ± 0.04. The genetic correlations between the traits were all moderate to high and positive (0.54 to 0.80); the phenotypic correlations between the traits were all moderate and positive (0.29 to 0.60). The standard errors of the heritabilities for neonatal traits, and for the genetic and phenotypic correlations between the traits, are low – indicating good precision and a well-developed and realized behavioral scoring system.

As the heritability of a trait is a prediction of future genetic response, so the moderate heritabilities of BA, LV and SA suggest that genetic solutions to improve these traits in Suffolk lambs are likely to lead to substantial progress. Interestingly, the heritabilities of the neonatal traits are higher than the range estimated for survival in Scottish Blackface lambs (0.18 - 0.33; SAWALHA *et al.* 2007), especially considering that all the neonatal traits are components of survival. There is the possibility that survival and fitness traits have not been actively selected for in the Suffolk for many generations, so that large variation for these traits could be expected. However, it is of note that survival is a less well-defined trait with many components, resulting possibly in lower heritability estimates. On the other hand, selecting for components of survival may be a more targeted, and potentially more successful, way to improve lamb survival, assuming the heritability of these components of survival is at least moderate.

In the present study, fixed effects were accounted for within the models fitted to estimate genetic parameters. Birth assistance was included in the model for lamb vigor and lamb vigor score was included in the model for sucking ability. Consequently, genetic parameters for lamb vigor score are independent of birth difficulty, and those for sucking ability are independent of birth assistance and lamb vigor score. Therefore, each neonatal trait can be improved individually; however, faster progress will be made if selection is based on multiple traits due to the genetic correlations between traits.

SMITH (1977) noted heritabilities for dystocia and lamb vigor at 0.13 ± 0.03 and 0.1 ± 0.03, respectively, and suggests that the low heritability for lamb vigor discourages its use as a selection tool for improved lamb survival. However, the lamb vigor scoring system used in this 1977 study was vague and subjective: 1 – strong, 2 – weak, 3 – very weak, 4 – died within 24 hours of birth, and may have been influenced by the previous experience of the scorer. In contrast, the lamb vigor scoring system developed by Matheson *et al.* (2011) was designed to describe specifically what behaviors lambs were expressing, rather than simply high or low vigor. Moreover, the genetic analysis in SMITH (1977) used a sire model, treating the neonatal traits as sire traits, whereas this study used an animal model and considered them as lamb traits. Perhaps the differences in realization of the scoring systems for lamb vigor and the models used explain the discrepancies between heritability for lamb vigor.

In this study, all neonatal traits were analyzed as lamb traits, even though BA and SA are composite traits, having maternal and offspring behavior components as well as measurements of human intervention. Lamb vigor, on the other hand, is strictly a lamb trait; previous studies have reported that lamb activity immediately after birth is largely independent of ewe behavior (DWYER and LAWRENCE 1999). Behavioral and fitness traits related to development are difficult to quantify and measure on farm. On research farms, latencies from birth to specific landmark behaviors are recorded (for examples see; DWYER *et al.* 1996; 2001; CLOETE *et al.* 2002; DWYER 2003; DWYER and LAWRENCE 2005b; CLOETE *et al.* 2006). Heritabilities for the latency from birth to standing have been estimated between 0.07 – 0.23 (CLOETE *et al.* 2002; CLOETE *et al.* 2006).

As previously noted, average heritabilities for fitness traits are not significantly different than heritabilities for behavioral traits (MOUSSEAU and ROFF 1987; STIRLING *et al.* 2002), possibly because so many fitness traits are composite traits, which include some form of behavior and/or morphological trait (PRICE and SCHLUTER 1991). In the domestic farm setting, selection is often on production traits and there is little or no active selection on fitness or behavior traits; whereas natural selection acting upon wild populations penalizes difficult birth, low vigor neonates or neonates with low sucking drive, or dams that do not allow neonates to nurse. Increased human intervention to maintain breeding animals with preferred production characteristics, regardless of neonatal behavior, may have resulted in artificially high genetic variation in these traits, therefore increasing heritabilities (e.g. as seen here for LV and SA, at 0.4 and 0.34, respectively).

5.4.3.2 Production genetic parameters

All production trait genetic analyses were conducted on a subset of the full data set of 11,092 lambs; all lambs included had a complete set of production records – W8WT, W20WT, UMD and UFD (2,885 records). For all production traits, the permanent environmental effect of the litter amounted to between 19-34% of the phenotypic variance, while direct additive genetic effects amounted to between 27-44% of the phenotypic variance (Table 5.8). The residual variance amounted to between 36-50% of the phenotypic variance. All heritabilities for production traits were in the moderate range (Table 5.8); W8WT, 0.27 ± 0.06; W20WT, 0.39 ± 0.07; UMD, 0.37 ± 0.06; and UFD, 0.44 ± 0.06. The genetic correlations between the traits were all moderate to high and positive (0.36-0.68), as were the phenotypic correlations (0.37-0.64). The heritabilities reported here are consistent with heritabilities for W20WT, UMD and UFD reported for three terminal-sire breeds (Charollais, Texel and Suffolk), 0.30 – 0.38 for W20WT, 0.29 – 0.32 for UMD, and 0.34 – 0.38 for UFD (JONES *et al.* 2004).

Table 5.8 Estimates of phenotypic variance (V_p), residual variance (V_r), genetic variance (V_g), permanent environmental effect of the litter (σ_{pe}^2), and heritabilities (in bold on diagonal), phenotypic correlations (above diagonal) and genetic correlations (below diagonal) for 8 week weight, 20 week weight, ultrasound muscle depth and ultrasound fat depth[1]

	8 week weight	20 week weight	Ultrasound muscle depth	Ultrasound fat depth
V_p	11.65 ± 0.37	45.38 ± 1.52	10.39 ± 0.34	1.99 ± 0.07
V_r	4.58 ± 0.49	17.82 ± 2.16	5.21 ± 0.50	0.72 ± 0.09
V_g	3.15 ± 0.76	17.66 ± 3.39	3.81 ± 0.73	0.88 ± 0.14
V_{pe}^2	3.92 ± 0.42	9.90 ± 1.58	1.37 ± 0.36	0.39 ± 0.07
8 week weight	**0.27** ± 0.06	0.59 ± 0.01	0.37 ± 0.02	0.38 ± 0.02
20 week weight	0.68 ± 0.09	**0.39** ± 0.07	0.64 ± 0.01	0.55 ± 0.02
Ultrasound muscle depth	0.39 ± 0.13	0.57 ± 0.09	**0.37** ± 0.06	0.46 ± 0.02
Ultrasound fat depth	0.36 ± 0.13	0.59 ± 0.08	0.55 ± 0.09	**0.44** ± 0.06

1 All standard errors (± s.e.) are given from a 4-variate model

5.4.3.3 Correlations between production traits and neonatal traits

All production trait genetic analyses were conducted on the production subset of the full data set (2,885 records); all lambs included had a complete set of neonatal and production records – BA, LV, SA, birth weight, W8WT, W20WT, UMD and UFD. It should be noted that the neonatal variances are smaller than the variances for the production traits. Metric production traits and fitness and behavior traits are measured in different units, with the difference probably due to differing levels of environmental variance rather than differing levels of genetic variation (PRICE and SCHLUTER 1991). Genetic and phenotypic correlations between the neonatal traits and production traits (Table 5.9) are not significantly different from zero, giving the unlikely suggestion that there is no link between neonatal fitness and future growth. It is possible that the large standard errors indicate that the sub-set of data used for production analysis was not powerful enough to estimate these parameters robustly (WILSON *et al.* 2010), therefore the estimated genetic and phenotypic correlations should be treated with the appropriate caution.

Table 5.9 Genetic (1) and phenotypic (2) correlations between neonatal traits (birth assistance, lamb vigour and sucking assistance) and performance traits (8 week weight, 20 week weight, ultrasound muscle depth and ultrasound fat depth)[1]

	Scores		
	Birth assistance	**Lamb vigour**	**Sucking assistance**
(1) Genetic correlations			
8 week weight	-0.03 ± 0.178	-0.24 ± 0.158	-0.07 ± 0.183
20 week weight	0.09 ± 0.164	-0.12 ± 0.148	-0.01 ± 0.170
Ultrasound muscle depth	0.20 ± 0.164	0.22 ± 0.185	0.22 ± 0.168
Ultrasound fat depth	0.12 ± 0.152	-0.07 ± 0.137	-0.04 ± 0.156
(2) Phenotypic correlations			
8 week weight	0.28 ± 0.102	0.02 ± 0.113	-0.26 ± 0.080
20 week weight	0.12 ± 0.104	0.05 ± 0.117	-0.11 ± 0.084
Ultrasound muscle depth	0.01 ± 0.092	0.01 ± 0.125	-0.11 ± 0.075
Ultrasound fat depth	0.00 ± 0.111	0.04 ± 0.123	-0.07 ± 0.089

1All standard errors (± s.e.) are given from a 7-variate model

This study has provided a comprehensive set of genetic (co)variances, including neonatal behavior and welfare traits (birth assistance, lamb vigor and sucking assistance) alongside production/performance traits (live weight at 8 and 20 weeks and ultrasound muscle and fat depths). This study also provided the opportunity to determine whether lambs with better neonatal behavior scores had improved production/performance in later life (up to 20 weeks). Lambs with low (good) neonatal fitness and behavior scores were more likely to be performance recorded than those with poorer scores. However, in-depth investigations into the relationship between the neonatal scores and production traits imply that differences in neonatal scores have no bearing on later production traits. One explanation for the apparent non-relationship between the different categories of neonatal scores and subsequent production traits may be that the poorest performing lambs had already been removed from the dataset. As previously mentioned, it is the breeders that submit the lamb data for inclusion into the BASCO data base at 8 weeks of age, based on live weight measurements, and again at 20 weeks, based on live weight and ultrasound muscle and fat depths. The poorest performing lambs will not be entered into the data base. Thus, at both of these points, the data set is skewed in favor of the lambs with better performance records. Therefore, only the highest performing lambs which had poor neonatal scores will be included in the production data set, biasing the results to show no relationship.

5.5 Conclusion

The heritability of lamb survival is commonly estimated to be essentially zero (YAPI *et al.* 1992; KONSTANTINOV *et al.* 1994; FOGARTY and GILMOUR 1998), suggesting that genetic progress in lamb survival is unlikely (CLOETE and SCHOLTZ 1998). However, in this study, we have reported moderate heritabilities for lamb fitness and behavior traits and show for the first time that these fitness and behavior traits have heritabilities comparable to those of production traits. It also demonstrates that moderate heritabilities are attainable when treated as a lamb trait rather than a sire or ewe trait, and thus show that selecting for components of survival response, rather than selection for survival itself, is a more targeted and potentially more successful way to improve survival.

CHAPTER SIX

INTERACTIONS BETWEEN NEONATAL BEHAVIOUR TRAITS AND FAECAL SOILING AT WEANING IN THREE BREEDS OF SHEEP

6.1 Abstract

Faecal soiling is one of the major factors predisposing sheep to cutaneous myiasis (commonly called ‘flystrike’). However, the basis of faecal soiling is not clearly understood and includes genetic and environmental factors. Early lamb development can affect future growth and may influence the later propensity to developing faecal soiling. The aim of this study was to investigate whether neonatal lamb traits relate to faecal soiling at weaning. The relationship between lamb sex, litter size, birth weight, birth assistance (BA), lamb vigour (LV), sucking assistance (SA) scores and weaning weight, growth rate and degree of faecal soiling (dag score) at ~15wk of age of a total of 382 lambs from 3 breeds were assessed. BA, LV and SA were scored from 0 to 4, with 0 the best and 4 the worst score.

Data were analysed using Restricted Maximum Likelihood (REML) in Genstat, rank transforming dag score prior to analysis; with BA, LV, SA, breed, sex and litter size as fixed effects, birth weight as a linear covariate and ewe as a random effect. Lambs with better LV had less faecal soiling at weaning (0 – 124.0 ±0.0, 1 – 166.1 ±7.2, 2 – 169.9 ±6.7, 3 – 239.9 ±10.4, 4 – 266.7 ±29.0; P<0.001), higher weaning weights (0 – 30.2 ±1.3, 1 – 31.1 ±0.5, 2 – 31.1 ±0.4, 3 – 28.5 ±0.6, 4 – 29.7 ±2.3; P=0.006) and higher growth rates (0 – 248 ±9.9, 1 – 263 ±4.1, 2 – 262 ±3.4, 3 – 224 ±5.0, 4 – 222 ±20.0; P<0.001). Single lambs had fewer dags than multiple litter lambs (1 – 168.9 ±7.8, 2 – 200.3 ±6.3, 3 – 193.1 ±15.7, 4 – 252.2 ±42.7; P=0.03). Lambs with less faecal soiling had higher weaning weights (0 – 31.0 ±0.3, 1 – 30.2 ±0.5, 2 – 26.7 ±1.8, 3 – 28.0 ±1.7, 4 – 24.9 ±1.2; P<0.001) and had the highest growth rates (0 – 261 ±2.6, 1 – 240 ±5.2, 2 – 215 ±11.4, 3 – 223 ±16.3, 4 – 183 ±10.0; P<0.001). These results suggest that early lamb development, specifically early vigour, is associated with reduced faecal soiling at weaning.

6.2 Introduction

Faecal soiling, i.e. the accumulation of faeces in the wool of the breech area (tail, perineum and anus), is one of the major factors predisposing sheep to cutaneous myiasis (flystrike). Faecal soiling is a result of watery faeces adhering to the long wool around the tail and breech area. Soiled wool clusters together into 'dags' and may also extend below the hock region. Although watery faeces are likely to have a multifactorial basis (SARGISON 2004), it has been suggested that they may arise from an increase in gut mobility, associated with host responses to internal parasite challenge (LARSEN *et al.* 1994; JACOBSON *et al.* 2009). Wet, sticky faeces are an ideal place for dipteran flies to lay eggs; maggots then hatch and feed directly on the tissues and blood of the sheep (TELLAM and BOWLES 1997) causing flystrike. A study by FRENCH *et al* (1996) indicates that the risk of flystrike increases by more than 20 times for every unit increase in faecal soiling, when measured as dag score (a scoring system for measuring faecal soiling in the breech area). In addition to welfare issues, lamb production is impaired, with growth rate negatively affected by the amount of faecal soiling (RODEN and HARESIGN 2008).

Faecal soiling also has economic effects on the sheep industry arising from wool and meat contamination. Whilst the estimated annual cost of gastrointestinal nematode parasitism to the UK sheep industry is £84 million (NIEUWHOF and BISHOP 2005), wool producers must deal with the cost of control, loss of wool and cleaning of fleeces (TELLAM and BOWLES 1997). The meat processing industry is concerned with the problem of faecal matter present on sheep carcasses arising from dags; carcass contamination is unavoidable (NEWTON *et al.* 1978) as pathogens and tissue-spoilage micro-organisms present on soiled wool are readily transferred to the carcass during processing (HADLEY *et al.* 1997).

The basis of faecal soiling is not clearly understood but includes both environmental and genetic factors. Increased faecal soiling is associated with the presence of long tails (FRENCH *et al.* 1994) and with longer wool, low 'crimp', fleeces (FRENCH and MORGAN 1996; FRENCH *et al.* 1998). Other contributing factors are low birth weight, being male, being born in a litter size greater than 2, neonatal diarrhoea, and being born to a dam with heavy faecal soiling (FRENCH and MORGAN 1996; FRENCH *et al.* 1998). For pre-weaning lambs, generalised out-breaks of faecal soiling usually indicate pathogenic infection, while sporadic faecal soiling is usually attributable to dietary issues (SARGISON 2004) or management problems (FRENCH and MORGAN 1996; FRENCH *et al.* 1998). In lambs less than 6 months old, the most common cause of faecal soiling is gastrointestinal parasites (SARGISON 2004).

Another factor which may be associated with the incidence of faecal soiling is neonatal development. Early life events have been known to affect future performance (LINDSTRÖM 1999) and immunity in later life (CARLIER and TRUYENS 1995). For example, ewe nutrition has an effect on foetal growth and subsequent lamb vigour after birth (DWYER 2003; DWYER *et al.* 2005), as well as on the level of parasitism in lambs (KIDANE *et al.* 2010) and faecal soiling (FRENCH and MORGAN 1996; FRENCH *et al.* 1998). Lambs with poor vigour (defined as the speed of neonatal behavioural progression) are slow to stand and slow to suck successfully (DWYER 2003). Delayed sucking affects survival due to reduced intake of colostrum, which is important for both nutritive and immunological status (PFEFFER *et al.* 2005). Therefore, the objective of this study was to investigate whether early development could be a contributory factor in the propensity to develop faecal soiling by assessing the relationship between specific neonatal traits and faecal soiling at weaning.

6.3 Methods and Materials

6.3.1 Animals

This study was approved by the SAC Animal Experiments and Ethics Committee. Data were collected from birth to weaning from lambs of 264 ewes, ranging in age from 2-7 years old: 32 Scottish Blackface (BF), 29 Suffolk (S) and 203 Texel (T). In total 383 lambs, born in 2008, were used: 43 BF lambs (20 males, 23 females; 20 singles, 23 twins), 49 S lambs (25 males, 24 females; 1 single, 43 twins, 5 triplets) and 291 T lambs (128 males, 163 females; 85 singles, 172 twins, 30 triplets, 4 quadruplets). Ewes were group-housed in straw-bedded large pens prior to lambing, and were fed *ad libitum* hay with a supplementary concentrate diet to satisfy 100% nutrient requirements.

Observers were present 24 h a day during lambing and all births were recorded live. All ewes were allowed to give birth unaided, as far as possible, according to a standard lambing protocol (DWYER and LAWRENCE 1998). The protocol permitted assistance if the birth process failed to progress, i.e. if no lamb parts were seen 1 h after the appearance of fluids and/or 2 h after lamb parts had been seen with no other obvious progress. Any intervention was kept to a minimum, correcting presentational difficulties where possible before allowing the ewe to continue unaided. Certain specific presentations (breech, head back and two lambs together) required immediate assistance. After birth ewes and lambs were moved to individual ‘mothering-up’ pens.

Lambs were scored for birth assistance, lamb vigour at 5 minutes of age and sucking assistance (Table 6.1) using scores developed previously (MATHESON *et al.* 2011). Lamb sex, litter size and birth weight were also recorded for each lamb within 2 hours of birth. In all instances, lambs were reared in their birth litters, with lambs from multiple litters reared as twins with only the lambs remaining with their dam used in the data set, with no cross-fostering of lambs; all male lambs were left entire. Ewes and lambs remained indoors for the first 3 days after birth and then were turned out to permanent pasture that was naturally infected with gastrointestinal parasites. Lambs were treated with ivermectin wormer only after weighing and dag scoring at weaning. At weaning (mean age 15 weeks), lambs were weighed and dag scored (Table 6.1d) using a similar scoring system as BISSETT and MORRIS (1996) and MORRIS *et al.* (2005). Growth rate to weaning was calculated as the difference between live weights at birth and weaning divided by the number of intervening days.

Table 6.1. Definitions of (a) birth assistance scores, (b) lamb vigour scores, (c) sucking assistance scores and (d) dag scores.

Score	Description
(a)	**Birth assistance scores**
0	Unassisted or easy uncomplicated delivery of short duration (<30 min)
1	Unassisted or easy uncomplicated delivery of long duration (>30 min)
2	Minor assistance required. Presentation corrected, little effort needed to deliver lamb
3	Major assistance required. Difficult delivery needing effort to deliver lamb
4	Veterinary assistance required
(b)	**Lamb vigour scores** (taken at 5 minutes of age)
0	Extremely active and vigorous lamb, has been standing on all 4 feet
1	Very active and vigorous lamb, standing on back legs and on knees
2	Active and vigorous lamb, on chest and holding head up
3	Weak lamb, lying flat, able to hold head up
4	Very weak lamb, unable to lift head, little movement
(c)	**Sucking assistance scores**
0	Lamb sucking well without assistance within 1 h of birth
1	Lamb sucking well without assistance within 2 h of birth
2	Lamb given sucking assistance/ fed by stomach tube once or twice in first 24 hours after birth
3	Lamb given sucking assistance, fed by stomach tube more than twice, needing help after 1 day old, but able to suck by 3 days old
4	Lamb still needing help to suck when more than 3 days old
(d)	**Dag scores**
0	No faecal soiling
1	Very light soiling
2	Light soiling and dags around anus
3	Moderate soiling and dags around anus and on legs
4	Extensive soiling and dags reaching down to hocks

6.3.2 Statistics

All data was analysed using Restricted Maximum Likelihood (REML) in Genstat (Genstat version 11.1.0.154; PAYNE *et al.* 2008). Dag score data were rank transformed prior to analysis and reported as mean rank (±s.e.). Rank transformation normalises the residuals of ordinal data as much as possible, allowing the use of linear models and estimation of fixed effects (CONOVER and IMAN 1981; WEISS 1986); this approach has also been used in previous studies using score data, for example ROOKE *et al*. (2009).

The linear models were developed in a step-down procedure, with non-significant main effects and interaction terms excluded from the final models. The exception to this was to include all the neonatal scores (birth assistance, lamb vigour and sucking assistance) as fixed effects, thereby allowing estimation of the effects of the neonatal scores on the weaning traits. Therefore, the main fixed effects were: breed, sex, and litter size, birth assistance score, lamb vigour score and sucking assistance score for birth weight, with a linear covariate of birth weight included for all other models. Interactions included in the model for dag rank were birth assistance score and sucking assistance score, and lamb vigour score and sucking assistance score. In addition, dag score was added as a fixed effect for weaning weight and growth rate from birth to weaning, and the interaction between dag score and breed. Ewe identity was fitted as a random effect for all models to account for lambs born in multiple litters. The statistical models used all converged but due to the unbalanced nature of the score data (Table 6.2), the models were over-parameterised and, consequently, unable to generate least square means. Therefore, pair-wise comparisons of the raw data, using either T tests or Welch tests, were performed to show significant differences between groups. For ease of understanding, the dag rank results were then back-transformed into the same scale as the original scoring system using logistic regression (logistic coefficient, 0.99963).

Table 6.2. Number of lambs within each category for: birth assistance, lamb vigour, sucking assistance and dag score.

Trait	Score category 0	1	2	3	4
Birth assistance	162	30	153	35	3
Lamb vigour	6	107	154	92	11
Sucking assistance	122	187	67	5	0
Dag score	247	94	20	9	11
Tied rank* value – dag score	124	295	352.5	367	377

*The ranking procedure gives the same rank to duplicate values and resumes ranking for subsequent numbers after leaving a gap in the numbering.

6.4 Results

6.4.1 Breed, lamb sex, litter size and birth weight effects

Table 6.3.1 presents the effects of breed on dag score, weaning weight and growth rate from birth to weaning. T lambs had lower dag scores and weighed more at weaning than both SB and S lambs. T lambs had a higher rate of growth than either S or SB lambs. Table 6.3.2 presents the effects of sex on dag score, weaning weight and growth rate from birth to weaning. Male lambs tended to have lower dag scores than females. Males tended to be heavier at weaning and had a significantly higher growth rate than females. Table 6.3.3 presents the effects of litter size on dag score, weaning weight and growth rate from birth to weaning. Single lambs had lower dag scores than lambs from multiple litters. Single lambs tended to weigh more at weaning and to have higher growth rates when compared to those from larger litters. There was no effect of birth weight on the amount of faecal soiling at weaning (Table 6.3.4). Lambs which were heavier at birth were heavier at weaning (Fig. 6.1a, parameter estimate ±s.e., 2.01 ±0.24; Wald=47.53, $P<0.001$) and had faster growth rates than lambs with a lower birth weight (Fig. 6.1b, parameter estimate ±s.e., 9.18 ±2.32; Wald=19.35, $P<0.001$).

Table 6.3. Effects of (1) breed, (2) lamb sex and (3) litter size on the weaning traits dag score, weaning weight and growth rate; (4) mean birth weight for each dag score category. Values for dag score are shown as mean rank (± s.e., with back-transformed values using logistic regression in parenthesis), values are mean (± s.e.) for live weight at weaning and growth rate. For all traits, pair-wise comparisons of the raw data, using either T tests or Welch tests, were performed to show significant differences between groups. Superscripts denote differences between the groups of *P*=0.05 or less.

	Breed				
(1) Trait	Scottish Blackface	Suffolk	Texel	Wald statistic	***P***
N	43	49	291		
Dag score	263.4 [a] ±14.3 (0.78)	301.4 [b] ±10.6 (1.06)	162.6 [c] ±4.4 (0.21)	80.02	<0.001
Weaning weight (kg)	28.1 [a] ±0.7	26.8 [a] ±0.9	31.2 [b] ±0.3	16.05	<0.001
Growth rate (g/day)	209 [a] ±5.0	200 [a] ±5.9	264 [b] ±2.4	174.83	<0.001

	Sex			
(2) Trait	Male	Female	Wald statistic	***P***
N	173	210		
Dag score	186.4 ±7.0 (0.34)	195.7 ±6.5 (0.39)	3.20	0.073
Weaning weight (kg)	30.9 ±0.4	29.9 ±0.3	2.95	0.086
Growth rate (g/day)	256 ±3.7	245 ±3.2	10.13	0.001

	Litter size					
(3) Trait	1	2	3	4	Wald statistic	***P***
N	106	238	35	4		
Dag score	168.9 [a] ±7.8 (0.25)	200.3 [b] ±6.3 (0.41)	193.1 [ab] ±15.7 (0.38)	252.2 [b] ±42.7 (0.71)	8.94	0.030
Weaning weight (kg)	33.1 [a] ±0.46	29.3 [b] ±0.34	29.4 [b] ±0.78	27.1 [b] ±1.59	7.39	0.060
Growth rate (g/day)	274 [a] ±4.2	240 [b] ±3.0	253 [b] ±6.5	240 [ab] ±11.5	15.21	<0.001

	Dag score category						
(4) Trait	0	1	2	3	4	Wald statistic	***P***
Birth weight (kg)	4.43 ±0.06	4.52 ±0.10	4.71 ±0.36	4.78 ±0.31	4.62 ±0.37	1.62	NS

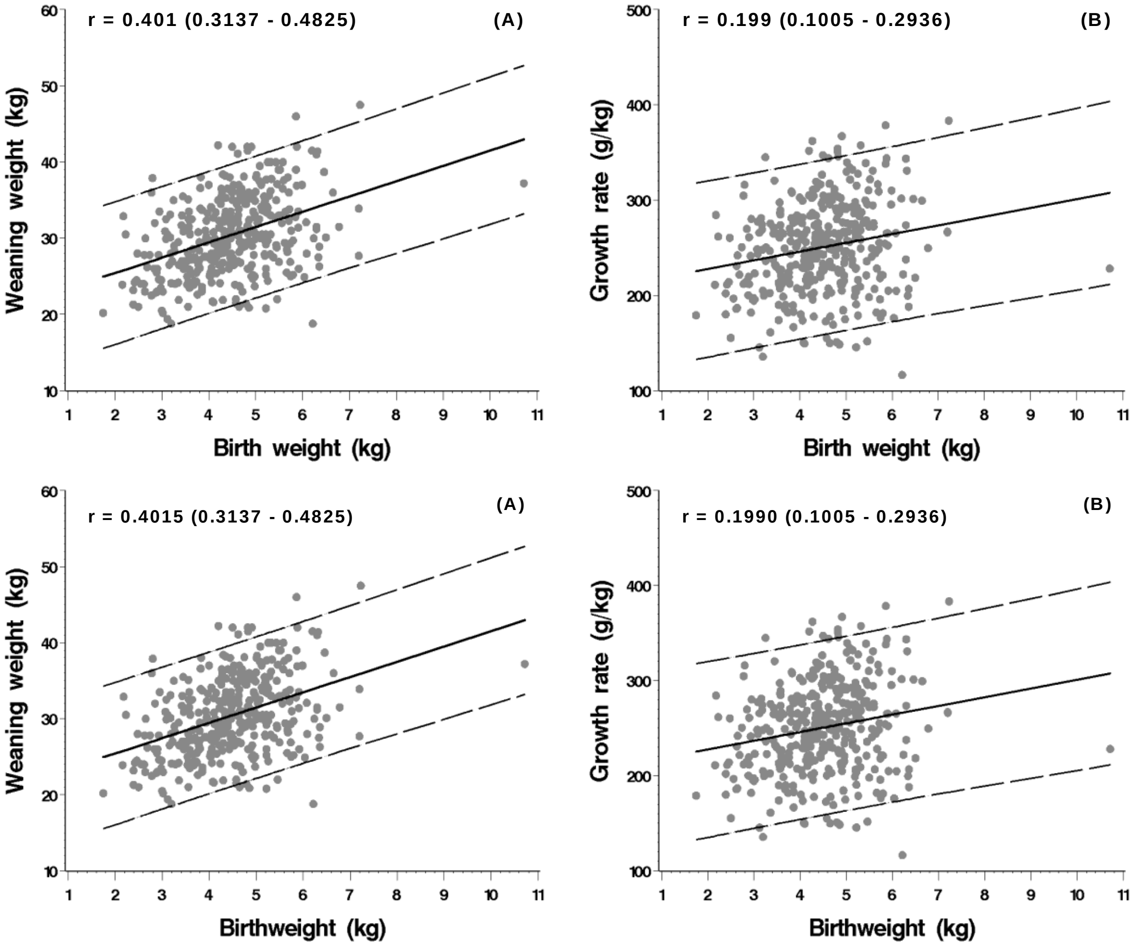


Figure 6.1. Regressions of weaning weight on **(A)** birth weight and **(B)** growth rate from birth to weaning (mean age at weaning = 15 weeks). Correlation coefficient and upper and lower confidence intervals are shown; dashed lines denote the 95% confidence interval of the regression line (solid line).

6.4.2 Relationship between neonatal traits and weaning traits

Lambs with a low birth assistance score had more faecal soiling (Table 6.4.1). There was no effect of birth assistance score on weaning weight or growth rate (Table 6.4.2 and 6.4.3). There was a significant relationship between lamb vigour score and dag rank, with lambs with better (lower) vigour scores having lower dag ranks (Table 6.4.1). Lambs with vigour scores of 0, 1 and 2 had greater live weights at weaning and higher growth rates than lambs with poorer vigour scores of 3 and 4 (Table 6.4.2 and 6.4.3). Somewhat surprisingly, lambs with a sucking assistance score of 0 had more faecal soiling than lambs with higher sucking assistance scores (Table 6.4.1).

There was also a birth assistance x sucking assistance interaction (Wald=4.95, P=0.026) and a lamb vigour score x sucking assistance interaction (Wald=6.25, P=0.012) with amount of faecal soiling. These interactions arise because not all birth assistance score categories (or lamb vigour categories) displayed the full range of sucking assistance categories, with the small numbers in subgroups introducing random differences. There was no effect of sucking assistance on either weaning weight or growth rate (Table 6.4.2 and 6.4.3).

Table 6.4. **(1)** Effects of neonatal scores at birth (birth assistance, lamb vigour and sucking assistance) on dag rank at weaning. Values are shown as mean rank (± s.e., with back-transformed values using logistic regression in parenthesis). **(2)** Effects of neonatal scores at birth (birth assistance, lamb vigour and sucking assistance) on live weight at weaning. **(3)** Effects of neonatal scores at birth on growth rate from birth to weaning. **(4)** Effects of dag score on weaning weight and growth rate from birth to weaning. Values are shown as mean (± s.e.). For all traits, pair-wise comparisons of the raw data, using either T tests or Welch tests, were performed to show significant differences between groups. Superscripts denote differences between the groups of *P*=0.05 or less.

	Score category						
(1) Dag rank	0	1	2	3	4	Wald statistic	***P***
Birth assistance	208.2 ^{ac} ±7.7 (0.46)	186.5 ^{ab} ±16.8 (0.34)	179.1 ^{b} ±7.1 (0.30)	161.9 ^{b} ±13.2 (0.21)	314.2 ^{c} ±19.2 (1.18)	11.24	<0.001
Lamb vigour	124.0 ^{a} ±0.0 (0)	166.1 ^{a} ±7.2 (0.23)	169.9 ^{a} ±6.7 (0.25)	239.9 ^{b} ±10.4 (0.63)	266.7 ^{b} ±29.0 (0.80)	72.27	<0.001
Sucking assistance	213.0 ^{a} ±9.4 (0.48)	185.9 ^{b} ±6.5 (0.34)	170.2 ^{b} ±9.9 (0.26)	158.2 ^{ab} ±34.2 (0.19)	-	6.46	0.011

	Score category						
(2) Weaning weight	0	1	2	3	4	Wald statistic	***P***
Birth assistance	29.2 ±0.4	28.6 ±.07	31.5 ±0.4	32.6 ±0.8	25.1 ±1.5	2.93	NS
Lamb vigour	30.2 ^{ab} ±1.3	31.1 ^{a} ±0.5	31.1 ^{a} ±0.4	28.5 ^{b} ±0.6	29.7 ^{ab} ±2.3	14.39	0.006
Sucking assistance	30.5 ±0.5	30.5 ±0.4	29.7 ±0.6	29.2 ±1.9	-	1.89	NS

	Score category						
(3) Growth rate	0	1	2	3	4	Wald statistic	***P***
Birth assistance	238 ±3.7	232 ±8.4	264 ±3.6	268 ±6.3	189 ±18.8	6.00	NS
Lamb vigour	248 ^{a} ±9.9	263 ^{a} ±4.1	262 ^{a} ±3.4	224 ^{b} ±5.0	222 ^{b} ±20.0	36.31	<0.001
Sucking assistance	246 ±4.6	251 ±3.4	255 ±5.0	266 ±26.2	-	1.78	NS

	Dag score						
(4)	0	1	2	3	4	Wald statistic	***P***
Weaning weight (kg)	31.0 ^{a} ±0.3	30.2 ^{ab} ±0.5	26.7 ^{bc} ±1.8	28.0 ^{abc} ±1.7	24.9 ^{c} ±1.2	28.23	<0.001
Growth rate (g/day)	261 ^{a} ±2.6	240 ^{b} ±5.2	215 ^{bc} ±11.4	223 ^{b} ±16.3	183 ^{c} ±10.0	65.67	<0.001

6.4.3 Relationship between faecal soiling, live weight at weaning and growth rate

Lambs with low dag scores had the heaviest weaning weights (Table 6.4.4) and the highest growth rates (Table 6.4.4). In both models there was an interaction between dag score x breed (weaning weight, Wald=50.98, $P<0.001$; growth rate, Wald=132.73, $P<0.001$). This interaction arises due to T lambs having few lambs with the worst (highest) dag scores, with the small numbers in subgroups introducing random differences.

6.5 Discussion

The results from this study show that neonatal lamb vigour appears to be associated with other traits later in life. This is suggested by the relationship between lamb vigour (at 5 minutes of age) and the amount of faecal soiling at weaning (at approximately 15 weeks of age), where lambs with good vigour scores have less faecal soiling. We also observed that lambs with greater faecal soiling have lower live weights at weaning, which is consistent with previous results (ALLERTON *et al.* 1998; BROUGHAN and WALL 2007). Additionally, lamb vigour (at 5 minutes of age) appears to be related to growth rate from birth to weaning, where with lambs with poorer vigour scores have lower growth rates.

As mentioned in the methods section, although the linear models used converged, due to the unbalanced nature of the score data, the models were over-parameterised and, consequently, unable to generate least square means for the fixed effects. This meant that simpler pair-wise comparisons of the raw data, using either T tests or Welch tests (dependent on whether the variances were equal or not), were performed to show significant differences between groups. Although using simple comparisons on the raw data does not allow for control of fixed effects for within-group means, the raw data means and least square means should point in the same direction for each of the fixed effects under investigation. For this reason, we think that the results reported here are worthy of further investigation.

6.5.1 Breed, lamb sex, litter size and birth weight effects

As expected, there was an effect of breed on dag score, live weight at weaning and growth from birth until weaning. That there are breed differences in growth rate and weaning weights are not surprising. The breed difference found in dag score, where Texel lambs have a much lower score than Scottish Blackface and Suffolk lambs, highlights the issue that the scoring system used may not be applicable across breeds. Texel lambs have legs with less wool compared to Scottish Blackface and Suffolk; therefore, Texel lambs could not be given the worst score. French and Morgan (1996) note that one of the primary factors for the extent of faecal soiling is the ability of the breech area to trap faecal material. However, this does not rule out the possibility that the breeds were actually different in their dag scores. Although faecal consistency scores were not collected during this study, it would be interesting for future work to include faecal consistency and egg counts. Many breeds are known to differ in their susceptibility to parasitism and dag scores (BISSET *et al.* 2001), however, those breeds with greater resistance to faecal soiling tend to be less productive than many European breeds (WOOLASTON and BAKER 1996).

The effects of sex on faecal soiling vary between studies; some studies report that females have more dags than males (BROUGHAN and WALL 2007) but other studies find the opposite (FRENCH *et al.* 1998) or no association at all (FRENCH and MORGAN 1996). While males were heavier than females at weaning, this did not reach statistical significance. However, there was a trend for males to be heavier than females which is consistent with literature (RANSOM and MULLANEY 1976; BENNETT *et al.* 1991; O'RIORDAN and HANRAHAN 1992) and to have higher growth rates, which is also in agreement with other studies (BENNETT *et al.* 1991; HAMMELL and LAFOREST 2000).

In this study, lambs from larger litters (twins and quadruplets but not triplets) were found to have greater faecal soiling than single lambs. This differs from the French and Morgan (1996) longitudinal study which followed lambs from birth to six months but is in agreement with a smaller study which was nested within the larger, longitudinal study (FRENCH *et al.* 1998). Lambs from larger litters are expected to start grazing at a younger age (VULICH *et al.* 1991) and would therefore be exposed to infected pasture sooner than single lambs. The effect of being born into a large litter carries over to weaning weight, with single lambs having greater weaning weights than those from multiple litters. This result is similar to that found in literature, with the biggest differences found between singles and twins than twins and other multiples (RANSOM and MULLANEY 1976; FOGARTY *et al.* 2000). Our data shows that multiple litter lambs have slower growth rates than single lambs and, thus, weigh less at weaning, which is similar to those found in other studies (BENNETT *et al.* 1991).

In this study we found no relationship between birth weight and faecal soiling, which differs from other studies which report a complex non-linear relationship (FRENCH and MORGAN 1996), where lambs with a birth weight over 5.2 kg developed faecal soiling at half the rate of lighter lambs. Low birth weight lambs had lower weaning weight and slower growth rates than lambs with higher birth weights. Again, this is in agreement with literature (SHELTON 1964).

6.5.2 Lamb vigour – sucking ability – faecal soiling relationship

Faecal soiling may be associated with gastro-intestinal parasitism; also, if high vigour lambs have superior immune systems to low vigour lambs, this suggests that high vigour lambs may be better able to deal with worm infection in later life. AHMAD *et al*. (2000) found that physically weak lambs had low serum immunoglobulin levels due to physically weak lambs being unable to suck or ingest enough colostrum. In addition, studies in calves have suggested that variation in vigour may account for observed variations in immunoglobulin levels (NORMAN *et al.* 1981; MUGGLI *et al.* 1984). If dag score correlates with the level of parasite exposure, this may explain the negative correlation between dag score and weaning weight, as parasite exposure and weight gain are negatively correlated (COOP *et al.* 1982). BROUGHAM and WALL (2007) found that increased levels of faecal soiling was linked with high faecal egg counts (FEC). Although, phenotypic correlations between FEC and live weights and growth rates are generally negative and close to zero, in lambs older than three months the genetic correlations are found to be >-0.85 (BISHOP *et al.* 1996; STEAR and BISHOP 1996). However, large scale epidemiological studies in the UK and Australia have found poor correlations between FEC and worm burden in adult sheep (MCKENNA 1981), suggesting that selection for reduced faecal soiling would not reduce worm burden. Conversely, in young lambs there is a good, reliable correlation between FEC and worm burden (STEAR *et al.* 2000). Indeed, STEAR *et al*. (2000) show that lambs which have a relatively low FEC after 3 months of age are likely to retain that advantage in later life. Studies have suggested that faecal soiling is a result of hypersensitivity to nematode challenge rather than a direct result of worm burden (LARSEN *et al.* 1994; JACOBSON *et al.* 2009). This would suggest that it is not worm burden *per se* affecting growth rate; rather, reduced growth rate occurs as a result of the body's response to parasite challenge/ exposure, i.e. the hypersensitivity leading to increased faecal soiling.

The positive relationships found between lamb vigour and dag scores may arise because high vigour lambs are quicker to stand and suck, which may result in greater intake of colostrum, which may, in turn, result in better immunity in early and later life (CARLIER and TRUYENS 1995; NOWAK and POINDRON 2006). The transfer of anti-nematode antibodies has been on record for some time (FILMER and MCCLURE 1951), more recently PFEFFER *et al.* (2005) reported that substantial quantities of colostral IgE were transferred to the lambs, showing IgE levels that were approximate to those found in the dam. This suggests that humeral immunity against gastro-intestinal nematode parasites and potentially other parasites in colostrum-fed lambs may approximate that of the ewe. A greater intake of colostrum may result in a healthier immune response but immunity gained against specific pathogens that the dam has been exposed to is finite in duration; French and Morgan (1996) found that maternally transferred immunity was negligible after lambs were 2-6 months of age. Therefore, there is still the possibility that although the lambs in this study were approximately 4 months old at weaning, they may have still retained some protection from their dam.

However, the negative relationship found between sucking assistance and dag scores suggests that a reduction in faecal soiling is not necessarily due to superior transfer of passive immunity *per se.* Indeed, BISHOP *et al*. (1996) suggest that lambs with most maternal antibodies are best protected at a young age, but may develop their own immunity more slowly or less effectively. It has been shown that as lambs grow older, the correlation between rate of growth and milk consumption decreases (BURRIS and BAUGUS 1955). Although this may offer an explanation why the sucking assistance score has no effect on either daily growth rate or live weight at weaning, a recent study demonstrated that lambs with better sucking assistance scores have significantly greater live weights, by almost 2 kg, at 21 weeks weights (MATHESON *et al.* in preparation).

Previous studies have shown that lambs that are more vigorous at birth are quicker and require less assistance to suck (DWYER 2003). Thus, a more vigorous lamb may stand and suck quickly and may result in a greater intake of colostrum and also facilitate the mother-young bonding process. Alexander and Williams (1966) showed that the peak of teat-seeking behaviour was not solely due to hunger and suggests that sucking behaviour was perhaps also used for mother-young bonding. VAL-LAILETT *et al* (2009) showed that colostrum-reward learning triggers mother-young bonding which is partly under the control of cholecystokinin (CCK) (DAUGÉ and LÉNA 1998). Plasma concentrations of CCK are low at birth, only increasing during and after sucking (NOWAK *et al.* 1997). Lambs prevented (or unable) to suck are unable to form a preference for their dam, whereas lambs which suck form a strong bond (NOWAK *et al.* 2001). Close mother-young relationships have been shown to facilitate learning of food preferences (MIRZA and PROVENZA 1992). Therefore, it would be reasonable to hypothesise that a lamb which is better bonded to its dam may have an increased opportunity to learn from her grazing decisions, including avoidance of faecal contaminated pasture (HUTCHINGS *et al.* 2002). This would reduce the risk of ingesting parasite larvae and, therefore, help to reduce incidence of faecal soiling (LARSEN *et al.* 1994; JACOBSON *et al.* 2009).

6.6 Conclusion

Our study has shown that poor vigour at birth is associated with increased amounts of faecal soiling at weaning, which in turn is associated with reduced weaning weight. Although our study was not designed to address the basis of this novel relationship, we hypothesised that higher vigour lambs, which stand and suck quickly, may be better bonded to their dams resulting in increased opportunities to learn to avoid faecal-contaminated pasture. The latter would reduce the risk for ingesting gastrointestinal parasite larvae, which consequently reduces parasitism-related faecal soiling.

CHAPTER SEVEN

GENERAL DISCUSSION

7.1 Chapter summaries

Chapter two presented the development of three scoring systems for neonatal traits. Detailed historical data were analysed for the development of the birth assistance score, which is a composite score based on how quickly a lamb was born, the ease with which it was born and the amount of human assistance required to be born. The lamb vigour score is a purely lamb behavioural trait, which is based on how far through behavioural progression a lamb has reached by 5 minutes of age. The sucking assistance score is also a composite score, based on how quickly a lamb reaches the udder and sucks, whether it manages to suck unaided or how much human assistance is required for the survival of the lamb. These scoring systems were then validated in a separate flock by simultaneously recording scores and the latency to perform certain landmark behaviours. The results obtained indicated that the scoring systems developed were a practical, valid and sensitive indicator of lamb fitness traits.

Chapter three presented a comparison between the neonatal traits for three purportedly divergent Suffolk strains, to investigate the possibility that there was sufficient difference between the strains to merit introgression of genes from one strain into another. The three strains compared were: UK high-index selected – animals of superior genetic merit as based on the Suffolk breeding objectives (8 and 21 week live weight, muscle and fat depth measured via ultrasound and mature live weight), UK Traditional – unselected, and NZ - selected in New Zealand through culling of animals with traits requiring extra labour and through performance recording. Sires from these strains were mated with Welsh Mountain ewes and the neonatal scores of the crossbred lambs recorded. The analysis indicated there was no significant effect of sire strain on any of the neonatal traits, and that the variation associated with individual sires was greater than the variation between the strains. These results suggest that introgressing genes from other Suffolk strains bred for easy lambing characteristics are not a viable option for improving neonatal traits.

Chapter four established whether the neonatal lamb fitness traits described in chapter two were heritable. Neonatal scores were recorded in an experimental flock of pure-bred Texel sheep for the purpose of estimating genetics parameters for each trait. Results indicated that heritabilities for all traits range from low to moderate, BA 0.43 (s.e. 0.06), LV 0.15 (s.e. 0.06), SA 0.27 (s.e. 0.04), suggesting there is sufficient genetic variation present within this Texel sub-population to allow for selection for improved neonatal fitness traits. This chapter also presented the effects of the Texel Muscling QTL (TM-QTL) on neonatal fitness traits. The results indicate that lambs inheriting one or two copies of the QTL, from either the sire or the dam, negatively impact upon the ability of a lamb to suck successfully. This suggests that selection for TM-QTL reduces a lamb's ability to survive without human assistance.

Chapter five established whether the scoring systems developed in chapter two were feasible, in a commercial setting, for the mass data collection needed for estimation of genetic parameters and the generation of estimated breeding values. This study also determined the relationship between neonatal traits and later production traits, with the future intention of integrating this data into breeding programmes. Lamb records from flocks belonging to the Industrial Partner for this PhD project, the Suffolk Sheep Society (UK), were analysed to report the genetic variance present within the UK population of registered pure-bred Suffolk sheep. The results from this analysis show that heritabilities were moderate for BA, 0.26 (s.e. 0.03), LV, 0.40 (s.e. 0.04) and SA, 0.32 (s.e. 0.03) with genetic correlations between neonatal traits all moderate to high and positive. This indicates that the developed and applied scoring methods have a good accuracy and demonstrates that neonatal fitness traits can have heritabilities comparable to those of production traits. The analysis also shows that neonatal survival traits of birth assistance and sucking assistance are moderately heritable, when treated as a lamb trait, indicating the selection should target the lambs in order to successfully, and efficiently, improve survival. The results also show a lack of correlation between neonatal traits and production traits, suggesting that selecting for improved neonatal traits in a breeding programme will not adversely affect production characteristics.

Chapter six presents a pilot study looking at whether neonatal lamb traits relate to faecal soiling at weaning. Neonatal scores were recorded at birth for lambs from three breeds of sheep (Scottish Blackface, Suffolk and Texel), then, at weaning, the lambs were scored for the amount of faecal soiling and weighed. This study suggested that lambs with poorer vigour at birth had higher levels of faecal soiling at weaning, which was, in turn, associated with a reduction in weaning weight. However, there should be further studies looking into this relationship within different breeds.

7.2 General discussion

As mentioned in chapter one, the management system in use on farm often dictates which type of lamb mortality is prevalent on farm; indoor systems suffer higher mortality due to infection (BINNS *et al.* 2002), with lamb mortality during parturition and the neonatal period minimised through supervision and assistance (NAWAZ and MEYER 1992), whereas outdoor systems suffer higher mortality from starvation or exposure to the weather (FISHER and MELLOR 2002) and perhaps predation (HAUGHEY 1993). It seems obvious to note that some aspects of welfare in extensive systems differ from intensive systems because the levels of human intervention, management systems and supply of nutrients are dramatically different (WATERHOUSE 1996). For instance, in Australia, a country which uses predominantly extensive systems, is it estimated 8.4 to 19.6 million lambs are lost to the economy every year (MELLOR and STAFFORD 2004). The number of lambs lost appears to be high but a recent study by ELLIOT *et al*. (2011) suggests that Australian producers have a positive attitude to improving lamb survival. Some of the management strategies currently used to reduce lamb mortality are: shelter belts for lambing (LYNCH *et al.* 1980), with a recent study showing the improved survival of twins due to increased shrub area (ROBERTSON *et al.* 2011); shearing ewes prior to lambing to induce shelter-seeking behaviour by ewes (NOWAK and POINDRON 2006); selection for calm temperament of the ewe (BICKELL *et al.* 2010); and, the use of lupins as a nutritional supplement for pregnant ewes (NOTTLE *et al.* 1998). In addition to the implementation of management strategies, there is an attempt to transfer knowledge of the latest research to producers, although participation at workshops is not entirely successful (ELLIOTT *et al.* 2011). However, it should be noted that none of these strategies for improving lamb survival involve selection on lamb behaviour. This may be because behaviour and fitness traits are often difficult to measure and frequently require prior knowledge of the behaviour. Ethograms are detailed behavioural descriptions for specific behaviours, painstakingly constructed through continuous observations, designed to increase objectivity. These observations are an accurate method for behavioural measurement but are difficult to record in large numbers due to the extensive labour requirements (MITLOEHNER *et al.* 2001). Once an ethogram has been constructed it is possible to record the time at which an animal performs a specific behaviour, and thus work out the duration of each behaviour or the latencies between behaviours. Many studies carried out on dedicated research farms have used time-based values for measuring lamb behaviour, for instance the latency between birth and standing or latency from birth to appearing to suck (ALEXANDER *et al.* 1990b; DWYER 2003; DWYER *et al.* 2005; BRIEN *et al.* 2009; ROOKE *et al.* 2009). Yet, similar to the continuous measurement method used to generate ethograms, timed behaviour traits are not easy nor quick to measure on-farm when compared to categorical indicator traits (BRIEN *et al.* 2009).

For genetic studies large numbers of animals are required to accurately estimate genetic correlations, since they are subjected to large sampling errors (ROFF 1997; LYNCH and ROFF 1998), but behavioural latency data are not easy to collect in large numbers. Therefore, categorical scoring systems are preferred. However, to be able to use a scoring system for selection purposes there must be a high degree of relatedness between the score and the underlying biology, i.e. the scoring methods need to have a high level of accuracy, precision and robustness. Not all visually scored traits have been found to relate to the underlying linear trait. For example, visually scored carcass conformation has a poor relationship to meat yield (NSOSO *et al.* 2000). For scoring systems to be an effective method of selection, scored traits need standardisation of the categories within them and knowledge of the relationship between scored traits and linear traits (JANSSENS and VANDEPITTE 2004). The scores developed in this thesis have been shown to be well-realised and biologically relevant scoring systems, capable of measuring neonatal fitness traits and evaluating management systems. However, the scores are not intended for use in comparisons across management systems. While the ethogram used for the development of the scores is the same regardless of where a lamb is, these scoring systems are valid only in an intensive management situation where people are present continuously to record scores. If there is nobody present to record a lamb's birth, any scores are meaningless for selection purposes.

The two possible approaches to genetic improvement of neonatal traits that are described in this thesis are: (i) introgression of genes from strains selected for easy-care traits (chapter three), and, (ii) intrabreed selection (chapter four, Texel, and chapter five, Suffolk). However, the data presented in Chapter 3 show that there was no significant difference in lamb vigour and sucking assistance between the three sire strains. In reality, there were greater differences between individual sires than between the different strains. Since line differences have been reported within single breeds (DWYER *et al.* 2001; CLOETE *et al.* 2002), and sire effects also reported within breed (DWYER *et al.* 2005). This would suggest that there is little evidence supporting approach (i) especially the perquisition of suitable genes in the genepool of other breeds, as the results of chapters four and five provide ample evidence that approach (ii) will be effective.

The large phenotypic variation shown in neonatal traits and the moderate heritabilities for neonatal traits suggest that approach (ii) is feasible. The data indicated that when behavioural measurements were biologically relevant and reliable the heritability of behaviour traits may be comparable to those of production traits. The analysis also showed that neonatal survival traits of birth assistance and sucking assistance are moderately heritable, when treated as a lamb trait rather than a sire or ewe trait, indicating the selection should target the lambs in order to successfully, and efficiently, improve survival. Some traits cannot be measured in an individual, for instance lambing ability in rams, and thus these traits must be inferred from the phenotypic values of female relatives. However, all lambs must be born and survive the neonatal period, so it would be better to use individual selection, where lambs are selected solely in accordance with their own phenotypic values. Individual selection is, operationally, the simplest method to use while returning the most rapid response (FALCONER and MACKAY 1996).

Selection acts simultaneously on several correlated life history traits (KELLY 1992), so a single trait may be under both direct and correlative selection. This would appear to be the case for all neonatal traits. Genetic correlations between traits explain how those traits co-vary. When the correlation is close to zero different genes control those traits. Conversely, when the correlations become different from zero, the traits share more genes. The genetic correlations presented for the Suffolk data are high (0.54 – 0.80) suggesting that the neonatal traits share more genes. The Texel data, on the other hand, have genetic correlations which do not appear to be significantly different from zero, it is possible that the large standard errors indicate that this data set has been pushed too far, meaning that the data set is too unbalanced at present (WILSON *et al.* 2010). Thus, if the correlations are high and positive, selection for one trait will correspondingly produce and increase in the other trait; but if the correlations are high and negative, selection for one trait will have a resultant decrease in the other trait. In this way negative correlations limit the scope of selection (STEARNS 1992).

For the Suffolk data presented in chapter five, the moderate neonatal heritabilities and moderate to high genetic correlations between the neonatal traits suggest that response to selection and the feasibility of genetic change within the Suffolk breed is high. Of course, this assumes the use of genetically superior animals within the breeding programme in order to gain genetic progress in crossbreeding and use of pure-bred animals, otherwise genetic progress may be slow (SNOWDER 2002). Thus, the individual sire differences in lamb vigour and sucking assistance reported in chapter three and the magnitude of reported heritabilities in reported in chapter five for the neonatal traits indicate that there is sufficient genetic variation present in the wider UK Suffolk population to improve neonatal traits through careful selection.

For the Texel data presented in chapter four, the moderate heritabilities for birth assistance and sucking assistance indicate that progress in these traits may be faster than in the lamb vigour trait, which has lower heritability, although if the phenotypic variance is high, progress may be rapid. As noted above, the genetic correlations between birth assistance and sucking assistance in the Texel data set are not significantly different from zero, which may suggest that an improvement in one trait would not result in a corresponding improvement in the other trait. On the other hand, the high genetic correlations between all the traits in the Suffolk data set suggest that an improvement in one trait brings a corresponding improvement in all neonatal traits. The difference in heritabilities in the neonatal traits between the Suffolk and Texel breeds may be due to either a smaller data set or is perhaps indicative of the difference in breeding objectives and the population under investigation. The heritability of a given trait refers to a particular population at a particular moment in time and values of a specific trait will be more or less the same depending on the environment and structure of the populations (FALCONER and MACKAY 1996). In this thesis, the genetic structure of the Texel data set is not the same as that of the Suffolk data set. In addition, anecdotally, Texel sheep have never been reported as having a problem with poor lamb vigour but have reported problems mainly with dystocia, where 2% of births require a caesarean section (DWYER and BUNGER in press). The Suffolk breed, on the other hand, is known to have issues with dystocia and poor lamb vigour. However, the moderate heritabilities presented in this thesis suggest that with intensive selection via breeding schemes incorporating all neonatal traits would result in good genetic progress.

An example of genetic progress in a composite trait would be intensive selection in the USA for litter weight weaned (litter weight weaning heritability, 0.10; SNOWDER 2002). This review reports that the litter weight weaned at 120 days old in four sheep breeds (Colombia, Polypay, Rambouillet and Targhee) over approximately 5 generations was 0.69 kg per breeding ewe, with a generation interval of 1.75 years (ERCANBRACK and KNIGHT 1985). This is an example which shows that even traits with low heritabilities can show a good response to selection due to the trait's large phenotypic variation coupled with intense selection of sires and dams with superior genetic merit (SNOWDER 2002). However, it must be noted that selection for major genes may create an imbalance among the component traits of reproduction and lamb survival (SNOWDER 2002). For instance, the Booroola allele will increase ovulation rate in sheep but it is also associated with a decrease in lamb survival (GOOTWINE *et al.* 2006).

7.3 Impact of genetic change

Before the mass movement of animals via international trade and the modernisation of animal husbandry, most animals were born, raised and subsequently reproduced in an environment that had shaped their ancestors for thousands of years (LINDSAY 1996). Reproductive behaviours would have been attuned to a specific environment and were geared to produce maximum numbers of offspring with the most efficiency. Nowadays, large numbers of animals have been transported to different and varied environments to which their ancestors had not been exposed. This is often because breeders wish to use the genetic merit of special characteristics found in those species; however, behavioural patterns have become more variable and are not necessarily ones which are conducive to an efficient reproductive outcome (LINDSAY 1996). Therefore, we should be asking if it is possible to understand the behavioural patterns of a species or breed and to then match that breed to an environment which maximises its productivity. This may appear to have been the case for Suffolk breeders in the UK over the past few decades. The increased use of intensive, indoor management to increase productivity resulted in large amounts of human intervention at parturition, since animals were increasingly bred for mature weight and conformation, and is an example of matching environment to the behaviour of the sheep. However, this change can also be reversed, as evidenced in the chapters of this thesis.

It must be noted that any genetic change in animal production results in biological change of the animal, often requiring changes in nutritional and management inputs for optimal genetic expression (SNOWDER 2002). However, if selection occurs in an optimum environment, and those animals are then moved to a sub-optimal environment, there will be a gap between the genetic potential of those animals and the phenotypic performance (SIMM 1998). Routine assistance at birth does not allow the phenotypic expression of ease of birth, so there is no measurement available for selection. A similar story can be said for the routine feeding of lambs by insertion of a tube into the stomach after birth (stomach-tubing). Not only is there the stress to the lamb, and ewe, from separation (DWYER 2008b) and from handling and application of the stomach-tube and disturbance of the ewe during or shortly after parturition, lambs with a full belly of milk/colostrum are satiated and less likely to perform the behaviours needed for adequate bonding with the ewe. Sometimes ewes are hand-milked for the colostrum (thereby inducing more stress from handling and milking of the ewe) but often lambs are fed stored, frozen or powdered colostrum which may mean that lambs are not provided with antibodies specific to the area that the lamb will be exposed to. In addition, enteral feeding increases the risk of infection of the stomach and oesophagus at each feed (HURRELL *et al.* 2009).

Anecdotally, these assistances have been considered ‘best practice’ because, while they are a considerable investment in terms of time and money (FISHER 2003), they reduce lamb mortality (NAWAZ and MEYER 1992; DWYER and LAWRENCE 2005a). Perhaps the next stage needs to be an education programme for stockmen to know when to restrict these practices unless they are required. Alternatively, if neonatal trait EBVs were included in breeding programmes and therefore such routine management practices were penalised, there may be an economic incentive for routine practices such as these to cease. In essence, since the scoring systems for birth assistance and sucking assistance are a composite of lamb and ewe behaviour and management practice, the scoring systems already penalise lambs with high scores. For example, a stockman who routinely gives a lamb colostrum via a feeding tube inserted into the stomach should be scoring a lamb as a 2 (lamb given sucking assistance/ fed by stomach tube once or twice in first 24 hours after birth). The lamb may have the genetic potential to have lower scores (lamb sucking well without assistance within 1 hour (0) or 2 hours (1)) except the lamb has not had the opportunity to express this trait and is thus the score is penalised for routine practice.

7.4 Early development and health traits at weaning

Early life events have been shown to affect both future performance (LINDSTRÖM 1999) and immunity in later life (CARLIER and TRUYENS 1995). For example, ewe nutrition has an effect on foetal growth and subsequent lamb vigour after birth (DWYER 2003; DWYER *et al.* 2005), as well as on the level of parasitism in lambs (KIDANE *et al.* 2010) and faecal soiling (FRENCH and MORGAN 1996; FRENCH *et al.* 1998). As we have seen, lambs with poor vigour are slow to stand and slow to suck successfully (DWYER 2003). This delayed sucking may affect survival due to reduced intake of colostrum, which is important for both nutritive and immunological status (PFEFFER *et al.* 2005). The results presented in the pilot study (chapter 6) suggest that an improvement in neonatal fitness traits, and specifically neonatal lamb vigour, would be associated with a corresponding improvement in faecal soiling at weaning and, possibly, an increase in weaning weight.

One of the unusual findings of this pilot study was that the Texel lambs had greater growth rates and weaning weights than the Suffolk lambs. A possible explanation could be that the data set used had substantially more Texel lambs than Suffolk lambs and suggests that the Suffolk data used in this study is unrepresentative of Suffolk growth traits in terms of Suffolk/Texel growth comparisons. However, the aim of this pilot study was to look at the relationship between neonatal lambs traits and later production traits (including dag score), and thus the inclusion of all lamb data in a single data set, with breed as a fixed effect, was considered appropriate. In addition to the breed difference in weight characteristics, there is anecdotal evidence that Texel lambs are cleaner, scour less and have lower faecal egg counts than Suffolk lambs (GOOD *et al.* 2006). It would have been interesting to have included faecal consistency in the range of data collected but, unfortunately, this data was not collected at the time. Should the study be repeated with a larger number of animals, then data collection will include faecal consistency as a measure.

Although the results from this pilot study are encouraging, there is concern that the data structure does not allow confident estimation of interaction terms, particularly where scores are involved. The fact that the data set was unbalanced meant that significant problems were encountered in the analysis, particularly with respect to determining significant effects. Unfortunately, when working with small datasets, the extremes of the scoring systems used are often not well represented. It would be hoped that this experiment could be repeated at a later time with greater numbers of lambs and, thus, be able to generate a greater range of score data.

7.5 Future directions

This thesis has concentrated on developing methods for measuring behaviour and providing tools for the genetic selection of animals with superior neonatal fitness traits. There are many future directions that may be followed to determine the relationship between the neonatal traits themselves and also between the neonatal traits and other health and welfare traits.

Unfortunately, there were insufficient numbers of animals in chapter four for partitioning the genetic variation into direct additive and maternal effects. Likewise, the structure of the data in chapter five did not allow for this partitioning of maternal and direct effects. This may have resulted in a slight over-estimation of the heritabilities presented in this thesis because the maternal component of the neonatal traits has been included in the heritability estimation. For example, CLOETE *et al*. (2002) reported that ease of parturition had higher estimates of maternal heritability than direct heritability, suggesting that inheritance for ease of parturition may be maternal. Future studies using more animals over more generations would allow for the teasing apart of these effects.

Further investigations into the relationship between neonatal lamb vigour and uptake of colostrum should be an interesting avenue of investigation. In the pilot study, lamb vigour was measured very early in life (5 minutes after birth) whereas antibody uptake from colostrum is seen over a relatively extended period. Although there are no studies looking at links between lamb vigour and colostrum uptake, a starting premise may be that more vigorous lambs absorb a higher level of antibodies.

Finally, it would be interesting to investigate the relationship between neonatal traits and the lambs' ability for learning. Previous studies have shown that lambs that are more vigorous at birth are quicker and require less assistance to suck (DWYER 2003). Thus, a more vigorous lamb may stand and suck quickly and may result in a greater intake of colostrum and also facilitate the mother-young bonding process. ALEXANDER AND WILLIAMS (1966) showed that the peak of teat-seeking behaviour was not solely due to hunger and suggests that sucking behaviour was perhaps also used for mother-young bonding. VAL-LAILETT *et al.* (2009) showed that colostrum-reward learning triggers mother-young bonding which is partly under the control of cholecystokinin (CCK) (DAUGÉ and LÉNA 1998). Plasma concentrations of CCK are low at birth, only increasing during and after sucking (NOWAK *et al.* 1997). Lambs prevented (or unable) to suck are incapable of forming a preference for their dam, whereas lambs which suck form a strong bond (NOWAK *et al.* 2001). Close mother-young relationships have been shown to facilitate learning of food preferences (MIRZA and PROVENZA 1992). Therefore, it would be reasonable to hypothesise that a lamb which is better bonded to its dam may have an increased opportunity to learn from her grazing decisions.

7.6 Conclusions

In conclusion, the work contained within this thesis shows that neonatal lamb behaviour traits can be measured accurately and easily using well-realised and biologically relevant scoring systems. Furthermore, these scoring systems are a feasible and practical method of measuring neonatal lamb vigour, which may be used to evaluate management systems and to improve selection criteria for neonatal traits. It has been shown that these traits are heritable and has also highlighted the issues of strain-selection when compared with individual phenotype selection. That these neonatal traits have, at worst, no effect on subsequent production characteristics (at 20 weeks of age) is suggestive that the traits could be incorporated into breeding indices with no loss of production output, although it may potentially reduce selection pressure on production traits. The information presented in this thesis is relevant to both farm animal welfare and to the genetic improvement of sheep breeds.

APPENDIX I

Appendix I is the basic analysis of the neonatal scores from Chapter 3 (Lambing ease and lamb vigour characteristics in lambs sired by rams of three Suffolk strains) with the removal of the covariate of birth weight and the fixed effects of the neonatal scores.

Appendix I

Table I.I. Least square means ± standard error for the ranks of the three neonatal behaviour scores (birth assistance, BA, lamb vigour, LV, and sucking assistance, SA) excluding the covariate of birth weight from the model. Within a column, means without a common superscript differ (P < 0.05).

Sire strain	N	BA rank	LV rank	SA rank
NZ		289.0 ± 21.6 ^{a}	269.8 ± 23.3 ^{a}	291.6 ± 19.5 ^{a}
UKH		332.0 ± 22.8 ^{b}	273.5 ± 25.0 ^{a}	269.9 ± 21.5 ^{a}
UKT		308.6 ± 23.0 ^{ab}	246.1 ± 25.2 ^{a}	273.9 ± 22.0 ^{a}
F value		3.35	1.14	0.9
P		*P*>0.05	*P*>0.05	*P*>0.05

Litter size at birth	N	BA rank	LV rank	SA rank
1		347.7 ± 27.1 ^{a}	260.7 ± 29.1 ^{a}	268.5 ± 26.1 ^{a}
2		267.8 ± 24.4 ^{b}	265.3 ± 25.2 ^{a}	292.1 ± 22.5 ^{a}
3		242.1 ± 27.6 ^{b}	240.3 ± 28.7 ^{a}	332.3 ± 27.0 ^{b}
4		381.8 ± 68.1 ^{ab}	284.8 ± 68.3 ^{a}	221.1 ± 26.0 ^{ab}
F value		10.21	0.63	2.85
P		<0.001	*P*>0.05	0.04

Lamb sex	N	BA rank	LV rank	SA rank
F		297.7 ± 21.4	254.6 ± 22.7	274.2 ± 19.3
M		322.0 ± 20.8	271.0 ± 22.0	282.8 ± 18.7
F value		4.81	1.81	0.81
P		0.03	*P*>0.05	*P*>0.05

Dam age (years)	N	BA rank	LV rank	SA rank
2		286.7 ± 24.5 ^{a}	279.9 ± 26.3	293.8 ± 23.5
3		313.1 ± 21.5 ^{ab}	252.4 ± 22.6	285.8 ± 19.8
4		329.8 ± 22.0 ^{b}	256.0 ± 23.3	256.0 ± 20.4
F value		2.67	0.99	2.55
P		*P*>0.05	*P*>0.05	*P*>0.05

Appendix I

Table I.II. Least square means ± standard error for the ranks of the three neonatal behaviour scores (birth assistance, BA, lamb vigour, LV, and sucking assistance, SA) excluding the covariate of birth weight from the model but including (A) birth assistance, for ranks of lamb vigour and sucking assistance, and (B) birth assistance score + lamb vigour score, for sucking assistance rank. Within a column, means without a common superscript differ (P < 0.05).

		(A)		**(B)**
Sire strain	N	LV rank	SA rank	SA rank
NZ	255	230.0 ± 24.1 [a]	306.8 ± 21.0 [a]	326.7 ± 24.2 [a]
UKH	205	297.1 ± 25.1 [a]	283.2 ± 22.1 [a]	302.6 ± 25.3 [a]
UKT	205	272.1 ± 25.5 [a]	286.9 ± 22.8 [a]	309.7 ± 25.2 [a]
F value		1.41	1.12	1.13
P		*P*>0.05	*P*>0.05	*P*>0.05
Litter size at birth	N	LV rank	SA rank	SA rank
1		280.0 ± 29.5 [a]	282.7 ± 26.5 [a]	302.7 ± 28.3 [a]
2		299.1 ± 26.4 [a]	303.8 ± 23.8 [ab]	326.1 ± 26.5 [ab]
3		275.6 ± 29.7 [a]	338.2 ± 28.0 [b]	359.0 ± 30.3 [b]
4		304.2 ± 67.4 [a]	244.5 ± 64.4 [ab]	264.0 ± 63.0 [a]
F value		0.72	2.10	2.29
P		*P*>0.05	*P*>0.05	*P*>0.05
Lamb sex	N	LV rank	SA rank	SA rank
F		282.9 ± 23.7	287.0 ± 20.6	308.8 ± 24.0
M		296.5 ± 22.9	297.6 ± 19.7	317.2 ± 22.8
F value		1.26	1.20	0.79
P		*P*>0.05	*P*>0.05	*P*>0.05
Dam age (years)	N	LV rank	SA rank	SA rank
2		310.2 ± 27.2	306.6 ± 24.5	323.5 ± 26.6
3		279.4 ± 23.5	300.3 ± 20.9	322.8 ± 34.3
4		279.58 ± 24.0	270.0 ± 21.3	292.6 ± 24.4
F value		1.42	2.58	2.44
P		*P*>0.05	*P*>0.05	*P*>0.05

APPENDIX II

Appendix II is the basic analysis of the neonatal scores from Chapter 4 (Genetic parameters for birth assistance in a pure-bred Texel population accounting for Texel double muscling QTL (TM-QTL) genotypes) with the removal of the covariate of birth weight and the fixed effects of the neonatal scores.

Table II.I. Least square Means (± standard error) for all traits measured at birth for known TM-QTL genotypes[1,2,3]; fixed effects were TM-QTL, litter size the lamb was born in to, lamb sex, dam age and year-farm rearing group. Maximum Likelihood Ratio χ^2 for whether a lamb needed assisted or not at birth. Values are given as actual observations (expected observations).

Trait	TM-QTL				*P*
	$+^S/+^D$	**$+^S/TM^D$**	**$TM^S/+^D$**	**TM^S/TM^D**	
N	52	25	74	45	
Birth weight	$3.80^{ab} \pm 0.23$	$3.48^{a} \pm 0.25$	$3.93^{b} \pm 0.20$	$3.97^{b} \pm 0.21$	*
Birth assistance	$0.76^{a} \pm 0.35$	$0.81^{a} \pm 0.39$	$1.11^{a} \pm 0.33$	$0.87^{a} \pm 0.37$	NS
Lamb vigour	$1.60^{a} \pm 0.28$	$1.60^{a} \pm 0.31$	$1.76^{a} \pm 0.27$	$1.83^{a} \pm 0.30$	NS
Sucking assistance	$0.80^{a} \pm 0.25$	$1.23^{b} \pm 0.28$	$1.30^{b} \pm 0.24$	$1.21^{b} \pm 0.26$	*
Not assisted at birth	20 (19.4)	13 (9.3)	20 (27.6)	20 (16.7)	†
Assisted at birth	32 (32.6)	12 (15.7)	54 (46.4)	25 (28.2)	

†$P < 0.10$, *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$

[1]TM-QTL legend: **$+^S/+^D$** = homozygous non carrier; **$+^S/TM^D$** = heterozygous carrier, inherited from the DAM; **$TM^S/+^D$** = heterozygous carrier, inherited from the SIRE; **TM^S/TM^D** = homozygous carrier

[2] Means within a column sharing a common superscript are not significantly different ($P > 0.05$)

[3] Lambs with unknown/partially known genotype (n=603) were not included in this analysis

Table II.II. Least square means (± standard error) for all traits measured at birth for litter size (a) and lamb sex (b)[1] for all lambs; fixed effects were TM-QTL, the interaction between TM-QTL and birth weight, litter size the lamb was born in to, lamb sex, dam age and year-farm rearing group. Maximum Likelihood Ratio χ^2 for whether a lamb needed assistance (1) or not (0) at birth. Values are given as actual observations (expected observations).

(a) Trait		**N**	**Assisted or not**		**Birth weight**	**Birth assistance**	**Lamb vigour**	**Sucking assistance**
			0	**1**				
Litter size	1	297	66 (128.2)	231 (168.8)	$5.71^{c} \pm 0.14$	$1.38^{a} \pm 0.20$	$1.66^{ab} \pm 0.14$	$1.12^{a} \pm 0.14$
	2	410	235 (177.0)	175 (233.0)	$4.72^{b} \pm 0.14$	$0.93^{b} \pm 0.18$	$1.52^{a} \pm 0.13$	$1.16^{a} \pm 0.13$
	3	88	41 (38.0)	47 (50.0)	$3.97^{a} \pm 0.16$	$1.36^{a} \pm 0.22$	$1.73^{b} \pm 0.16$	$1.39^{b} \pm 0.15$
	4	4	3 (1.7)	1 (2.3)	$4.11^{ab} \pm 0.40$	$0.58^{ab} \pm 0.54$	$0.96^{a} \pm 0.39$	$0.87^{ab} \pm 0.38$
P			***		***	***	*	†

(b) Trait		**N**	**Assisted or not**		**Birth weight**	**Birth assistance**	**Lamb vigour**	**Sucking assistance**
			0	**1**				
Lamb sex	Male	368	-	-	4.71 ± 0.17	1.13 ± 0.22	1.53 ± 0.16	1.15 ± 0.16
	female	431	-	-	4.54 ± 0.17	1.00 ± 0.22	1.41 ± 0.16	1.12 ± 0.16
P					**	NS	*	NS

†$P < 0.10$, *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$
[1] Means within a column sharing a common superscript are not significantly different ($P > 0.05$)

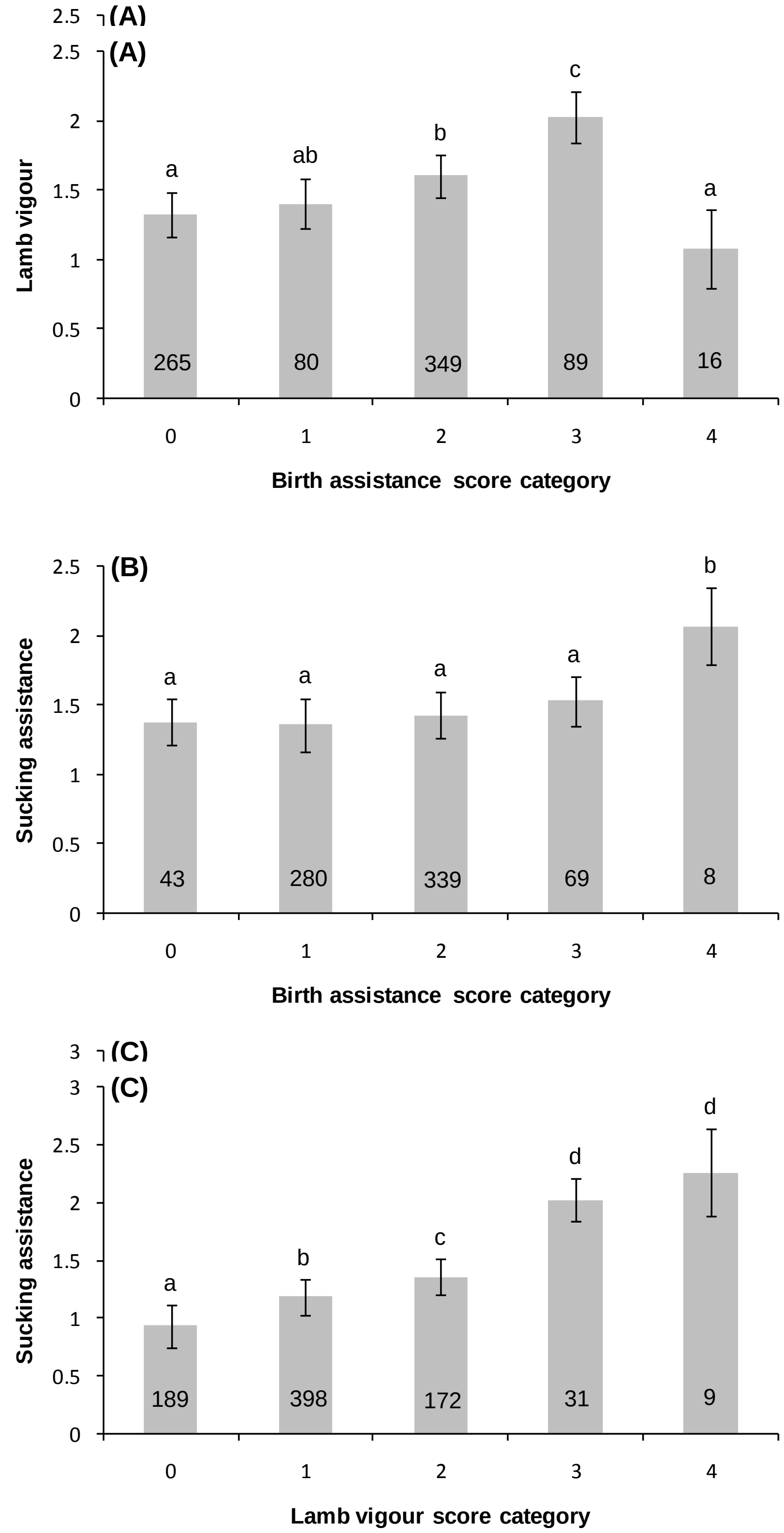


Figure II.I. Relationships between neonatal scores (excluding the covariate of birth weight; least square means ± s.e.): birth assistance and lamb vigour **(A)**; birth assistance and sucking assistance **(B)**; and, lamb vigour and sucking assistance **(C)**. Columns indicate the number of lambs in each score category. Means sharing a common character in their superscript do not differ significantly (P>0.05).

APPENDIX III

Appendix III is the basic analysis of the neonatal scores from Chapter 5 (Genetic parameters for fitness and neonatal behaviour traits in Suffolk sheep) with the removal of the covariate of birth weight and the fixed effects of the neonatal scores.

Table III.I. Relationship between season of birth and the neonatal scores (birth assistance, lamb vigour and sucking assistance, excluding the covariate of birth weight. Lambs from season 1 were born between Dec-Feb; lambs from season 2 were born between Mar-June. Predicted mean ± s.e. for the neonatal scores are from 11092 animals.

	Trait	Season		
		1	**2**	***P***
(1)	N	9530	1562	
Birth assistance		2.39 ± 0.14	2.34 ± 0.15	NS
Lamb vigour		2.30 ± 0.12	2.21 ± 0.12	*
Sucking assistance		2.41 ± 0.13	2.38 ± 0.13	NS

†*P* < 0.10, **P* < 0.05, ****P* < 0.001.

Table III.II. Effect of litter size on the neonatal scores (birth assistance, lamb vigour and sucking assistance, excluding the covariate of birth weight. Predicted mean ± s.e. for neonatal scores are from 11092 animals.[1]

(1)	Litter size			
	1	**2**	**3**	**4**
N	2546	7067	1419	55
Birth assistance	2.56 ^{a} ± 0.10	2.38 ^{b} ± 0.10	2.42 ^{b} ± 0.10	2.32 ^{ab} ± 0.18
Lamb vigour	2.18 ^{a} ± 0.08	2.22 ^{b} ± 0.08	2.36 ^{c} ± 0.08	2.71 ^{d} ± 0.15
Sucking assistance	2.19 ^{a} ± 0.09	2.30 ^{b} ± 0.09	2.52 ^{c} ± 0.09	3.10 ^{d} ± 0.16

[1] Within a row, means sharing a common character in their superscript do not differ significantly (*P*>0.05).

Table III.III. Relationship between lamb sex and the neonatal scores (birth assistance, lamb vigour and sucking assistance, excluding the covariate of birth weight. Predicted mean ± s.e. for the neonatal scores are from 11092 animals.

	Trait	Sex		
		Male	**Female**	***P***
(1)	N	9530	1562	
Birth assistance		2.40 ± 0.15	2.33 ± 0.15	***
Lamb vigour		2.27 ± 0.12	2.24 ± 0.12	*
Sucking assistance		2.39 ± 0.13	2.40 ± 0.13	NS

†*P* < 0.10, **P* < 0.05, ****P* < 0.001.

Appendix III

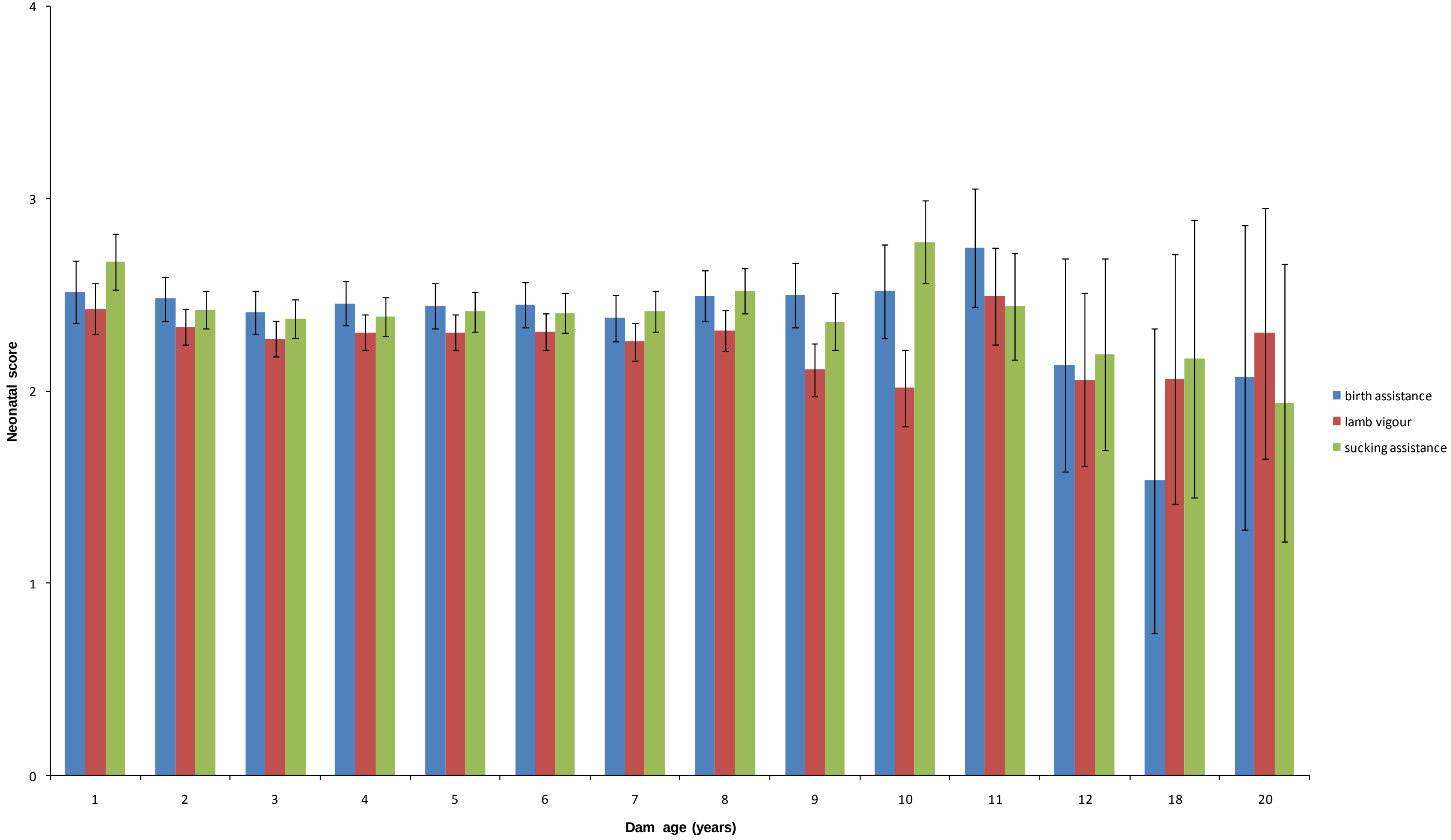


Figure III.I. Relationship between the neonatal scores (birth assistance, lamb vigour and age of dam (years), excluding the covariate of birth weight. Predicted mean ± s.e. for the neonatal scores are from 11092 animals.

REFERENCES

AFOLAYAN, R. A., N. M. FOGARTY, A. R. GILMOUR, V. M. INGHAM, G. M. GAUNT *et al.*, 2008 Reproductive performance and genetic parameters in first cross ewes from different maternal genotypes. Journal of Animal Science **86:** 804-814.

AFOLAYAN, R. A., N. M. FOGARTY, V. M. INGHAM, A. R. GILMOUR, G. M. GAUNT *et al.*, 2007 Genetic evaluation of crossbred lamb production. 3. Growth and carcass performance of second-cross lambs. Australian Journal of Agricultural Research **58:** 457-466.

AFRC, 1993 *Energy and protein requirements of ruminants. An advisory manual prepared by the AFRC Technical Committee on Responses to Nutrients*. CAB International, Wallingford, UK.

AHMAD, R., A. KHAN, M. T. JAVED and I. HUSSAIN, 2000 The level of immunoglobulins in relation to neonatal lamb mortality in Pak-Karakul sheep. Veterinarski Arhiv **70:** 129-139.

AL-JAWAD, A. B., and J. L. LEES, 1985 Effects of ewe's colostrum and various substitutes on the serum concentration, gut closure process and growth rate of lambs. Animal Production **40:** 123-127.

ALEXANDER, G., 1988 What makes a good mother? Proceedings of the Australian Society for Animal Production **17:** 25-41.

ALEXANDER, G., D. STEVENS and L. R. BRADLEY, 1988 Maternal behaviour in ewes following caesarian section. Applied Animal Behaviour Science **19:** 273-277.

ALEXANDER, G., D. STEVENS and L. R. BRADLEY, 1990a Distribution of field birth-sites of lambing ewes. Australian Journal of Experimental Agriculture **30:** 759-767.

ALEXANDER, G., D. STEVENS and L. R. BRADLEY, 1990b Intensive Observations During Lambing in a Goiter-Affected Flock, with Special Reference to Behavior of Lambs. Australian Journal of Experimental Agriculture **30:** 749-757.

ALEXANDER, G., D. STEVENS, L. R. BRADLEY and S. A. BARWICK, 1990c Maternal behaviour in Border Leicester, Glen Vale (border leicester derived) and Merino sheep. Australian Journal of Experimental Agriculture **30:** 27-38.

ALEXANDER, G., and D. WILLIAMS, 1966 Teat-seeking activity in lambs during the first hours of life. Animal Behaviour **14:** 166-176.

ALEXANDER, G., and D. WILLIAMS, 1968 Shivering and non-shivering thermogenesis during summit metabolism in young lambs. Journal of Physiology **198:** 251-276.

ALLERTON, G. R., R. P. GOGOLOWSKI, D. RUGG, R. E. PLUE, R. A. BARRICK *et al.*, 1998 Field trials evaluating ivermectin controlled-release capsules for weaner sheep and for breeding ewes. Australian Veterinary Journal **76:** 39-43.

AMER, P. R., G. J. NIEUWHOF, G. E. POLLOTT, T. ROUGHSEDGE, J. CONINGTON *et al.*, 2007 Industry benefits from recent genetic progress in sheep and beef populations. Animal **1:** 1414-1426.

ANNETT, R. W., L. E. R. DAWSON, H. EDGAR and A. F. CARSON, 2009 Effects of source and level of fish oil supplementation in late pregnancy on feed intake, colostrum production and lamb output of ewes. Animal Feed Science and Technology **154:** 169-182.

BAXTER, E. M., S. JARVIS, R. B. D'EATH, D. W. ROSS, S. K. ROBSON *et al.*, 2008 Investigating the behavioural and physiological indicators of neonatal survival in pigs. Theriogenology **69:** 773-783.

BELL, M. J., and D. J. ROBERTS, 2007 Effect of twinning on the feed intake, performance and health of dairy cows. Livestock Science **107:** 274-281.

BENNETT, G. L., A. H. KIRTON, D. L. JOHNSON and A. H. CARTER, 1991 Genetic and environmental effects on carcass characteristics of Southdown x Romney lambs: I. Growth rate, sex, and rearing effects. Journal of Animal Science **69:** 1856-1863.

BIANCHI, G., G. GARIBOTTO and O. BENTANCUR, 2001 Lamb survival, growth characteristics, carcass weight and GR values in pure Corriedale and Texel, Hampshire Down, Southdown and Suffolk sired heavy lambs. Archivos de Medicina Veterinaria (Valdivia) **33:** 261-268.

BICKELL, S. L., R. NOWAK, P. POINDRON, D. FERGUSON and D. BLACHE, 2010 Maternal behaviour at parturition in outdoor conditions differs only moderately between single-bearing ewes selected for their calm or nervous temperament. Animal Production Science **50:** 675-682.

BINNS, S. H., I. J. COX, S. RIZVI and L. E. GREEN, 2002 Risk factors for lamb mortality on UK sheep farms. Preventive Veterinary Medicine **52:** 287-303.

BISHOP, S. C., K. BAIRDON, Q. A. MCKELLAR, M. PARK and M. J. STEAR, 1996 Genetic parameters for faecal egg count following mixed, natural, predominantly *Osteragia circumcinta* infection and relationships with live weight in lambs. Animal Science **63:** 423-128.

BISSET, S. A., and C. A. MORRIS, 1996 Feasibility and implications of breeding sheep for resilience to nematode challenge. International Journal for Parasitology **26:** 857-868.

BISSET, S. A., C. A. MORRIS, J. C. MCEWAN and A. VLASSOFF, 2001 Breeding sheep in New Zealand that are less reliant on anthelmintics to maintain health and productivity. New Zealand Veterinary Journal **49:** 236-246.

BOMAN, I. A., G. KLEMETSDAL, O. NAFSTAD, T. BLICHFELDT and D. I. VÅGE, 2011 Selection based on progeny testing induces rapid changes in myostatin allele frequencies – a case study in sheep. Journal of Animal Breeding and Genetics **128:** 52-55.

BORG, R. C., D. R. NOTTER and R. W. KOTT, 2009 Phenotypic and genetic associations between lamb growth traits and adult ewe body weights in western range sheep. Journal of Animal Science **87:** 3506-3514.

BRADFORD, G. E., 1972 The role of maternal effects in animal breeding: VII. Maternal effects in sheep. Journal of Animal Science **35:** 1324-1334.

BRAMBELL, F. W. R., 1970 *The transmission of passive immunity from mother to young*. North Holland Publishing, London.

BRIEN, F. D., M. L. HEBART, J. E. HOCKING-EDWARDS, J. C. GREEFF, K. W. HART *et al.*, 2009 Genetics of lamb survival: Preliminary studies of the Information Nucleas flock, pp. 108-111 in *Proceeding of the Association for the Advancement of Animal Breeding and Genetics*, Barossa Valley, South Australia.

BRIEN, F. D., M. L. HEBART, D. H. SMITH, J. E. H. EDWARDS, J. C. GREEFF *et al.*, 2010 Opportunities for genetic improvement of lamb survival. Animal Production Science **50:** 1017-1025.

BROUGHAN, J. M., and R. WALL, 2007 Faecal soiling and gastrointestinal helminth infection in lambs. International Journal for Parasitology **37:** 1255-1268.

BROWNRIDGE, P., 1995 The nature and consequences of childbirth pain. European Journal of Obstetrics Gynecology and Reproductive Biology **59:** S9-S15.

BRYANT, E. H., 1986 On Use of Logarithms to Accommodate Scale. Systematic Zoology **35:** 552-559.

BURRIS, M. J., and C. A. BAUGUS, 1955 Milk Consumption and Growth of Suckling Lambs. Journal of Animal Science **14:** 186-191.

BYRNE, T. J., P. R. AMER, P. F. FENNESSY, A. R. CROMIE, T. W. J. KEADY *et al.*, 2010 Breeding objectives for sheep in Ireland: A bio-economic approach. Livestock Science **132:** 135-144.

CAMPBELL, S. G., M. J. SIEGEL and B. J. KNOWLTON, 1977 Sheep immunoglobulins and their transmission to neonatal lamb. New Zealand Veterinary Journal **25:** 361-365.

CARLIER, Y., and C. TRUYENS, 1995 Influence of maternal infection on offspring resistance towards parasites. Parasitology Today **11:** 94-99.

CARPENTER, C. E., O. D. RICE, N. E. COCKETT and G. D. SNOWDER, 1996 Histology and composition of muscles from normal and callipyge lambs. Journal of Animal Science **74:** 388-393.

CARROLL, J. A., A. M. GAINES, J. D. SPENCER, G. L. ALLEE, H. G. KATTESH *et al.*, 2003 Effect of menhaden fish oil supplementation and lipopolysaccharide exposure on nursery pigs - I. Effects on the immune axis when fed diets containing spray-dried plasma. Domestic Animal Endocrinology **24:** 341-351.

CASSEL, B., 2009 Using Heritability for Genetic Improvement, pp. 404-084. Virginia Cooperative Extension, Virginia Tech, and Virginia State University.

CHUCRI, T. M., J. M. MONTEIRO, A. R. LIMA, M. L. B. SALVADORI, J. R. KFOURY *et al.*, 2010 A review of immune transfer by the placenta. Journal of Reproductive Immunology **87:** 14-20.

CIMEN, M., and M. KARAALP, 2009 Effect of restricted suckling time on milk components and sucking behavior of lambs. Archiv Fur Tierzucht-Archives of Animal Breeding **52:** 299-308.

CLOETE, S. W. P., 1992 Observation on litter size, parturition and maternal behavior in relation to lamb mortality in fecund dormer and South-African mutton merino ewes. South African Journal of Animal Science-Suid-Afrikaanse Tydskrif Vir Veekunde **22:** 214-221.

CLOETE, S. W. P., I. MISZTAL and J. J. OLIVIER, 2009 Genetic parameters and trends for lamb survival and birth weight in a Merino flock divergently selected for multiple rearing ability. Journal of Animal Science **87:** 2196-2208.

CLOETE, S. W. P., and A. J. SCHOLTZ, 1998 Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for multiple rearing ability. Australian Journal of Experimental Agriculture **38:** 801-811.

CLOETE, S. W. P., A. J. SCHOLTZ, J. J. E. CLOETE and J. B. VAN WYK, 2005 The ability of Merino ewes and lambs to reunite after separation, as affected by divergent selection for ewe multiple rearing capacity. Australian Journal of Experimental Agriculture **45:** 1131-1137.

CLOETE, S. W. P., A. J. SCHOLTZ, A. R. GILMOUR and J. J. OLIVIER, 2002 Genetic and environmental effects on lambing and neonatal behaviour of Dormer and SA Mutton Merino lambs. Livestock Production Science **78:** 183-193.

CLOETE, S. W. P., J. B. VAN WYK, A. J. SCHOLTZ and A. R. GILMOUR, 2006 Genetic parameters and trends for lamb behaviour, pp. Communication 17-07 in *Proceedings of the 8th World Congress on Genetics Applied to Livestock Production*, Belo Horizonte, Brazil.

CONINGTON, J., S. C. BISHOP, A. WATERHOUSE and G. SIMM, 2004 A bioeconomic approach to derive economic values for pasture-based sheep genetic improvement programs. Journal of Animal Science **82:** 1290-1304.

CONINGTON, J., J. COLLINS and C. DWYER, 2010 Selection for easier managed sheep. Animal Welfare **19:** 83-92.

CONOVER, W. J., and R. L. IMAN, 1981 Rank transformations as a bridge between parametric and nonparametric statistics. American Statistician **35:** 124-129.

COOP, R. L., A. R. SYKES and W. K. ANGUS, 1982 The effect of three levels of intake of Ostertagia circumcincta larvae on growth rate, food intake and body composition of growing lambs. Journal of Agricultural Science **98:** 247-255.

CORDOBA, R., S. PKIYACH, J. A. ROOKE, S. A. EDWARDS, P. C. PENNY *et al.*, 2000 *The effect of feeding salmon oil during pregnancy on causes of piglet deaths prior to weaning*. British Society of Animal Science {a} , Penicuik, Midlothian, EH26 0RZ, UK.

DA COSTA, M., A. SCHMIDEK and L. M. TOLEDO, 2008 Mother-offspring interactions in Zebu cattle. Reproduction in Domestic Animals **43:** 213-216.

DAUGÉ, V., and I. LÉNA, 1998 CCK in Anxiety and Cognitive Processes. Neuroscience & Biobehavioral Reviews **22:** 815-825.

DAWSON, L. E. R., and A. F. CARSON, 2002 Effects of crossbred ewe genotype and ram genotype on ewe prolificacy, lamb viability and lamb output in the lowland sector. Journal of Agricultural Science **139:** 169-181.

DESAI, M., and C. N. HALES, 1997 Role of fetal and infant growth in programming metabolism in later life. Biological Reviews **72:** 329-348.

DICKINSON, A. G., J. L. HANCOCK, G. J. R. HOVELL, C. S. TAYLOR and G. WIENER, 1962 The size of lambs at birth - a study involving egg transfer. Animal Science **4:** 64-79.

DONALD, H. P., and W. S. RUSSELL, 1970 The relationship between live weight of ewe at mating and weight of newborn lamb. Animal Science **12:** 273-280.

DWYER, C., and L. BUNGER, in press Factors affecting dystocia and offspring vigour in different sheep genotypes. Preventive Veterinary Medicine.

DWYER, C. M., 2003 Behavioural development in the neonatal lamb: Effect of maternal and birth-related factors. Theriogenology **59:** 1027-1050.

DWYER, C. M., 2008a Genetic and physiological determinants of maternal behaviour and lamb survival: implications for low input sheep management. Journal of Animal Science **86** E246-E258.

DWYER, C. M., 2008b The welfare of the neonatal lamb. Small Ruminant Research **76:** 31–41.

DWYER, C. M., and H. L. I. BORNETT, 2004 Chronic stress in sheep: assessment tools and their use in different management conditions. Animal Welfare **13:** 293-304.

DWYER, C. M., S. K. CALVERT, M. FARISH, J. DONBAVAND and H. E. PICKUP, 2005 Breed, litter and parity effects on placental weight and placentome number, and consequences for the neonatal behaviour of the lamb. Theriogenology **63:** 1092-1110.

DWYER, C. M., and A. B. LAWRENCE, 1997 Induction of maternal behaviour in non-pregnant, hormone-primed ewes. Animal Science **65:** 403-408.

DWYER, C. M., and A. B. LAWRENCE, 1998 Variability in the expression of maternal behaviour in primiparous sheep: Effects of genotype and litter size. Applied Animal Behaviour Science **58:** 311-330.

DWYER, C. M., and A. B. LAWRENCE, 1999 Does the behaviour of the neonate influence the expression of maternal behaviour in sheep? Behaviour **136:** 367-389.

DWYER, C. M., and A. B. LAWRENCE, 2000 Effects of maternal genotype and behaviour on the development of their offspring in sheep. Behaviour **137:** 1629-1654.

DWYER, C. M., and A. B. LAWRENCE, 2005a Frequency and cost of human intervention at lambing: an interbreed comparison. Veterinary Record **157** 101-104.

DWYER, C. M., and A. B. LAWRENCE, 2005b A review of the behavioural and physiological adaptations of hill and lowland breeds of sheep that favour lamb survival. Applied Animal Behaviour Science **92:** 235-260.

DWYER, C. M., A. B. LAWRENCE and S. C. BISHOP, 2001 The effects of selection for lean tissue content on maternal and neonatal lamb behaviours in Scottish Blackface sheep. Animal Science **72:** 555-571.

DWYER, C. M., A. B. LAWRENCE, S. C. BISHOP and M. LEWIS, 2003 Ewe–lamb bonding behaviours at birth are affected by maternal undernutrition in pregnancy. British Journal of Nutrition **89:** 123-136.

DWYER, C. M., A. B. LAWRENCE, H. E. BROWN and G. SIMM, 1996 Effect of ewe and lamb genotype on gestation length, lambing ease and neonatal behaviour of lambs. Reproduction, Fertility and Development **8:** 1123-1129.

DWYER, C. M., and K. L. MORGAN, 2006 Maintenance of body temperature in the neonatal lamb: Effects of breed, birth weight, and litter size. Journal of Animal Science **84:** 1093-1101.

EALES, F. A., and J. SMALL, 1981 Effects of colostrum on summit metabolic rate in Scottish Blackface lambs at five hours old. Research in Veterinary Science **30:** 266-269.

ELLIOTT, J., J. SNEDDON, J. A. LEE and D. BLACHE, 2011 Producers have a positive attitude toward improving lamb survival rates but may be influenced by enterprise factors and perceptions of control. Livestock Science **140:** 103-110.

ERCANBRACK, S. K., and A. D. KNIGHT, 1985 Lifetime (7 years) production of 1/4 and 1/2 Finnish Landrace ewes from Rambouillet, Targhee and Colombia ewes under range conditions. Journal of Animal Science **61:** 66-77.

EVERETT-HINCKS, J. M., N. LOPEZ-VILLALOBOS, H. T. BLAIR and K. J. STAFFORD, 2005 The effect of ewe maternal behaviour score on lamb and litter survival. Livestock Production Science **93:** 51-61.

EVERITT, G. C., and K. E. JURY, 1966 Effects of sex and gonadectomy on growth and development of Southdown x Romney cross lambs. 2. Effects on carcass grades, measurements and chemical composition. Journal of Agricultural Science **66:** 15-&.

FALCONER, D. S., and T. F. C. MACKAY, 1996 *Introduction to Quantitative Genetics*. Addison Wesley Longman Limited, Harlow.

FAURE, J. M., 1994 Behavioural genetics–an overview, pp. 20, 129 in *Proceedings of the 5th World Congress of Genetics Applied to Livestock Production*, Guelph, Ontario, Canada.

FILMER, D. B., and T. J. MCCLURE, 1951 Absorption of anti-nematode antibodies from ewes colostrum by the new-born lamb. Nature **168:** 170-170.

FISHER, M., 2003 New Zealand farmer narratives of the benefits of reduced human intervention during lambing. Journal of Agricultural and Environmental Ethics **16:** 77-90.

FISHER, M., and D. J. MELLOR, 2002 The welfare implications of shepherding during lambing in extensive New Zealand farming systems. Animal Welfare **11:** 157-170.

FISHER, R. A., 1930 *The genetical theory of natural selection.* Clarendon Press, Oxford.

FLINN, L. D., and J. V. WHITEMAN, 1974 Reproductive performance of Dorset x Western ewes when mated to Dorset or Blackface rams. Journal of Animal Science **39:** 18-24.

FOGARTY, N. M., and A. R. GILMOUR, 1998 Heritability and repeatability estimates and correlations of lamb mortality with birth weight and litter size, pp. 55-58 in *Proceedings of the 6th World Congress of Genetics Applied to Livestock Production*, 11-16 January 1998, Armidale, NSW, Australia.

FOGARTY, N. M., D. L. HOPKINS and R. V. D. VEN, 2000 Lamb production from diverse genotypes 1. Lamb growth and survival and ewe performance. Animal Science **70:** 135-145.

FOGARTY, N. M., and J. M. THOMPSON, 1974 Relationship between pelvic dimensions, other body measurements and dystocia in Dorset Horn ewes. Australian Veterinary Journal **50:** 502-506

FRASER, A. F., and D. M. BROOM, 1998 Early behaviour and parental behaviour, pp. 198-255 in *Farm Animal Behaviour and Welfare*. CAB International, Wallingford.

FRASER, A. F., and M. TERHUNE, 1977 Radiographic studies of postural behaviour in the sheep fetus: I. Simple fetal movements. Applied Animal Ethology **3:** 221-234.

FRENCH, N. P., E. BERRIATUA, G. KAYA and K. L. MORGAN, 1998 Case control study of diarrhoea and faecal soiling in two- to six-month-old lambs. Veterinary Record **143:** 408-412.

FRENCH, N. P., and K. L. MORGAN, 1996 Role of neonatal and maternal risk factors in the faecal soiling of lambs. Veterinary Record **139:** 460-465.

FRENCH, N. P., T. D. H. PARKIN and K. L. MORGAN, 1996 A case control study of blowfly strike in lambs. Veterinary Record **139:** 384-388.

FRENCH, N. P., R. WALL and K. L. MORGAN, 1994 Lamb tail docking: a controlled field study of the effects of tail amputation on health and productivity. Veterinary Record **134:** 463-467.

GIANOLA, D., and J. L. FOULLEY, 1983 Sire evaluation for ordered categorical data with a threshold model. Genetics Selection Evolution **15:** 1-23.

GILMOUR, A. R., B. R. GULLIS, S. J. WELHAM and R. THOMPSON, 2006 *ASReml User Guide Release 2.0*. VSN International Ltd, Hemel Hempstead, UK.

GODDARD, P., 2011 Sheep, pp. 178-251 in *Management and Welfare of Farm Animals: The UFAW Farm Handbook; 5th Edition*, edited by J. WEBSTER. Universities Federation for Animal Welfare (UFAW).

GONYOU, H. W., and J. M. STOOKEY, 1985 Behavior of parturient ewes in group-lambing pens with and without cubicles. Applied Animal Behaviour Science **14:** 163-171.

GOOD, B., J. P. HANRAHAN, B. A. CROWLEY and G. MULCAHY, 2006 Texel sheep are more resistant to natural nematode challenge than Suffolk sheep based on faecal egg count and nematode burden. Veterinary Parasitology **136:** 317-327.

GOOTWINE, E., A. ROZOV, A. BOR and S. REICHER, 2006 Carrying the FecB (Booroola) mutation is associated with lower birth weight and slower post-weaning growth rate for lambs, as well as a lighter mature bodyweight for ewes. Reproduction Fertility and Development **18:** 433-437.

GREEFF, J. C., E. SAFARI, N. M. FOGARTY, D. L. HOPKINS, F. D. BRIEN *et al.*, 2008 Genetic parameters for carcass and meat quality traits and their relationships to liveweight and wool production in hogget Merino rams. Journal of Animal Breeding and Genetics **125:** 205-215.

GREENBERG, A. J., H. MCNAMARA and W. W. MCCRORY, 1966 Metabolic balance studies in primary renal tubular acidosis: Effects of acidosis on external calcium and phosphorus balances. The Journal of Pediatrics **69:** 610-618.

GREENWOOD, P. L., A. S. HUNT, J. W. HERMANSON and A. W. BELL, 2000 Effects of birth weight and postnatal nutrition on neonatal sheep: II. Skeletal muscle growth and development. Journal of Animal Science **78:** 50-61.

GROMMERS, F. J., L. ELVING and P. VAN ELDIK, 1985 Parturition difficulties in sheep. Animal Reproduction Science **9:** 365--374.

HADLEY, P. J., J. S. HOLDER and M. H. HINTON, 1997 Effects of fleece soiling and skinning method on the microbiology of sheep carcases. Veterinary Record **140:** 570-574.

HAMMELL, K. L., and J. P. LAFOREST, 2000 Evaluation of the growth performance and carcass characteristics of lambs produced in Quebec. Canadian Journal of Animal Science **80:** 25-33.

HARVILLE, D. A., and R. W. MEE, 1984 A Mixed-Model Procedure for Analyzing Ordered Categorical Data. Biometrics **40:** 393-408.

HAUGHEY, K. G., 1980 The effect of birth injury to the foetal nervous system on the survival and feeding behaviour of lambs. Reviews in Rural Science (Australia) **4:** 109-111.

HAUGHEY, K. G., 1993 Perinatal Lamb Mortality - Its Investigation, Causes and Control (Reprinted from Journal of the South-African Veterinary Association, Vol 62, Pg 78-91, 1991). Irish Veterinary Journal **46:** 9-28.

HAUGHEY, K. G., J. M. GEORGE and B. J. MCGUIRK, 1985 The repeatability of rearing performance of Merino and Dorset Horn ewes and its relationship with mature pelvic size. Australian Journal of Experimental Agriculture **25:** 541-549.

HENDERSON, N. O., 1990 Quantitative Genetic Analysis of Neurobehavioural Phenotypes, pp. 283-287 in *Developmental Behaviour Genetics: Neural,* *Biomedical and Evolutionary Approaches*, edited by M. E. HAHN, J. K. HEWIT and N. D. HENDERSON. Oxford University Press, Oxford, New York.

HERPIN, P., M. DAMON and J. LE DIVIDICH, 2002 Development of thermoregulation and neonatal survival in pigs. Livestock Production Science **78:** 25-45.

HINCH, G. N., 1997 Genetics of Behaviour, pp. 353-374 in *The Genetics of Sheep*, edited by L. R. PIPER and A. RUVINSKY. CAB, New York.

HINCH, G. N., S. F. CROSBIE, R. W. KELLY, J. L. OWENS and G. H. DAVIS, 1985 Influence of birthweight and litter size on lamb survival and litter size in high fecundity Booroola-Merino crossbred flocks. New Zealand Journal of Agricultural Research **28:** 31-38.

HINCH, G. N., G. H. DAVIS, S. F. CROSBIE, R. W. KELLY and R. W. TROTTER, 1986 Causes of lamb mortality in two highly prolific Booroola crossbred flocks and a Romney flock. Animal Reproduction Science **12:** 47-61.

HOHENBOKEN, W. D., 1985 Inheritance and importance of behavioral traits in livestock, pp. 146-161 in *Proceedings of the 34th Annual Meeting of the Poultry Breeders of America* St Louis, Missouri.

HUBER, T. L., 1976 Physiological Effects of Acidosis on Feedlot Cattle. Journal of Animal Science **43:** 902-909.

HURRELL, E., E. KUCEROVA, M. LOUGHLIN, J. CAUBILLA-BARRON, A. HILTON *et al.*, 2009 Neonatal enteral feeding tubes as loci for colonisation by members of the Enterobacteriaceae. BMC Infectious Diseases **9**.

HUTCHINGS, M. R., J. M. MILNER, I. J. GORDON, I. KYRIAZAKIS and F. JACKSON, 2002 Grazing decisions of Soay sheep, *Ovis aries*, on St Kilda: a consequence of parasite distribution? Oikos **96:** 235-244.

JACKSON, S. P., R. D. GREEN and M. F. MILLER, 1997 Phenotypic characterization of rambouillet sheep expressing the callipyge gene: I. Inheritance of the condition and production characteristics. Journal of Animal Science **75:** 14-18.

JACOBSON, C. L., K. BELL and R. B. BESIER, 2009 Nematode parasites and faecal soiling of sheep in lairage: evidence of widespread potential production losses for the sheep industry. Animal Production Science **49:** 326-332.

JANSSENS, S., and W. VANDEPITTE, 2004 Genetic parameters for body measurements and linear type traits in Belgian Bleu du Maine, Suffolk and Texel sheep. Small Ruminant Research **54:** 13-24.

JENKINSON, C. M. C., S. W. PETERSON, D. D. S. MACKENZIE, M. F. MCDONALD and S. N. MCCUTCHEON, 1995 Seasonal effects on birth weight in sheep are associated with changes in placental development. New Zealand Journal of Agricultural Research **38:** 337-345.

JOHANSON, J. M., and P. J. BERGER, 2003 Birth Weight as a Predictor of Calving Ease and Perinatal Mortality in Holstein Cattle. Journal of Dairy Science **86:** 3745-3755.

JOHNSON, W., L. PENKE and F. M. SPINATH, 2011 Heritability in the Era of Molecular Genetics: Some Thoughts for Understanding Genetic Influences on Behavioural Traits. European Journal of Personality **25:** 254-266.

JONES, H. E., R. M. LEWIS, M. J. YOUNG and G. SIMM, 2004 Genetic parameters for carcass composition and muscularity in sheep measured by X-ray computer tomography, ultrasound and dissection. Livestock Production Science **90:** 167-179.

JORGENSEN, J. N., 1994 Estimation of genetic-parameters for litter size in sheep using a nonlinear method. Acta Agriculturae Scandinavica Section a-Animal Science **44:** 8-11.

KELLY, C. A., 1992 Spatial and temporal variation in selection on correlated life-history traits and plant size in *Chamaecrista fasciculata*. Evolution **46:** 1658-1673.

KERSLAKE, J. I., J. M. EVERETT-HINCKS and A. W. CAMPBELL, 2005 Lamb survival: a new examination of an old problem. Proceedings of the New Zealand Society of Animal Production **65:** 13-18.

KIDANE, A., J. G. M. HOUDIJK, S. ATHANASIADOU, B. J. TOLKAMP and I. KYRIAZAKIS, 2010 Effects of maternal protein nutrition and subsequent grazing on chicory (*Cichorium intybus*) on parasitism and performance of lambs. Journal of Animal Science **88:** 1513-1521.

KILGOUR, R. J., and K. G. HAUGHEY, 1993 Pelvic size in Merino ewes selected for lamb rearing ability is greater than that of unselected Merino ewes. Animal Reproduction Science **31:** 237-242.

KINGSOLVER, J. G., H. E. HOEKSTRA, J. M. HOEKSTRA, D. BERRIGAN, S. N. VIGNIERI *et al.*, 2001 The Strength of Phenotypic Selection in Natural Populations. The American Naturalist **157:** 245-261.

KNIGHT, T. W., P. R. LYNCH, D. R. H. HALL and H. U. P. HOCKEY, 1988 Identification of Factors Contributing to the Improved Lamb Survival in Marshall Romney Sheep. New Zealand Journal of Agricultural Research **31:** 259-271.

KONSTANTINOV, K. V., G. J. ERASMUS and J. B. VANWYK, 1994 Evaluation of Dormer sires for litter size and lamb mortality using a threshold model. South African Journal of Animal Science-Suid-Afrikaanse Tydskrif Vir Veekunde **24:** 119-121.

LAMBE, N. R., J. CONINGTON, S. C. BISHOP, A. WATERHOUSE and G. SIMM, 2001 A genetic analysis of maternal behaviour score in Scottish Blackface sheep. Animal Science **72**
415-425.

LARSEN, J. W. A., N. ANDERSON, A. L. VIZARD, G. A. ANDERSON and H. HOSTE, 1994 Diarrhoea in Merino Ewes During Winter - Association with Trichostrongylid Larvae. Australian Veterinary Journal **71:** 365-372.

LAWRENCE, A. B., J. CONINGTON and G. SIMM, 2004 Breeding and animal welfare: practical and theoretical advantages of multi-trait selection. Animal Welfare **13:** S191-S196.

LINDSAY, D. R., 1996 Environment and reproductive behaviour. Animal Reproduction Science **42:** 1-12.

LINDSTRÖM, J., 1999 Early development and fitness in birds and mammals. Trends in Ecology & Evolution **14:** 343-348.

LOPEZ-VILLALOBOS, N., and D. J. GARRICK, 1999 Genetic parameter estimates for lamb survival in Romney sheep. Proceedings of the New Zealand Society of Animal Production **59:** 121-124.

LYNCH, J. J., B. E. MOTTERSHEAD and G. ALEXANDER, 1980 Sheltering behaviour and lamb mortality amongst shorn Merino ewes lambing in paddocks with a restricted area of shelter or no shelter. Applied Animal Ethology **6:** 163-174.

LYNCH, M., and D. A. ROFF, 1998 *Genetics and the analysis of quantitative traits*. Sinauer Associates, Sunderland.

MACFARLANE, J. M., N. R. LAMBE, S. C. BISHOP, O. MATIKA, E. RIUS-VILARRASA *et al.*, 2009a Effects of the Texel muscling quantitative trait locus on carcass traits in crossbred lambs. Animal **3:** 189-199.

MACFARLANE, J. M., N. R. LAMBE, O. MATIKA, K. A. MCLEAN, A. Y. MASRI *et al.*, 2010a Texel loin muscling QTL (TM-QTL) located on ovine chromosome 18 appears to exhibit imprinting and polar overdominance, pp. in *9th World Congress on Genetics applied to Livestock production*, Leipzig, Germany.

MACFARLANE, J. M., S. M. MATHESON and C. M. DWYER, 2009b Genetic parameters for birth difficulty, lamb vigour and lamb sucking ability in Suffolk sheep, pp. in *UFAW International Symposium 2009: Darwinian selection, selective breeding and the welfare of animals*, University of Bristol, Bristol, UK.

MACFARLANE, J. M., S. M. MATHESON and C. M. DWYER, 2010b Genetic parameters for birth difficulty, lamb vigour and lamb sucking ability in Suffolk sheep. Animal Welfare **19:** 99-105.

MALLARD, E. C., S. REES, M. STRINGER, M. L. COCK and R. HARDING, 1998 Effects of chronic placental insufficiency on brain development in fetal sheep. Pediatric Research **43:** 262-270.

MARÍA, G. A., K. G. BOLDMAN and L. D. VAN VLECK, 1993 A note on heritability estimates for growth traits in male and female Romanov sheep. Animal Science **57:** 326-328.

MARNET, P. G., and B. C. MCKUSICK, 2000 Regulation of milk ejection and milkability in small ruminants. Livestock Production Science **70:** 125-133.

MATHESON, S. M., J. M. MACFARLANE, L. BUNGER and C. M. DWYER, 2010 Genetic parameters for neonatal lamb traits in Suffolk sheep, pp. in *Proceedings of the 44th International Society for Applied Ethology*, Uppsala, Sweden.

MATHESON, S. M., J. M. MACFARLANE, L. BUNGER and C. M. DWYER, in preparation Genetic parameters for neonatal behaviour and welfare traits in Suffolk sheep.

MATHESON, S. M., J. A. ROOKE, K. MCILVANEY, M. JACK, S. ISON *et al.*, 2011 Development and validation of on-farm behavioural scoring systems to assess birth assistance and lamb vigour. Animal **5:** 776-783.

MATIKA, O., R. PONG-WONG, J. A. WOOLLIAMS, J. LOW, G. J. NIEUWHOF *et al.*, 2006 Verifying quantitative trait loci for muscle depth in commercial terminal sire sheep, pp. 22-10 in *Proceedings of the 8th World Congress on Genetics Applied to Livestock Production*, Belo Horizonte, Minas Gerais, Brazil.

MAXA, J., E. NORBERG, P. BERG and J. PEDERSEN, 2007 Genetic parameters for growth traits and litter size in Danish Texel, Shropshire, Oxford Down and Suffolk. Small Ruminant Research **68:** 312-317.

MCKENNA, P. B., 1981 The diagnostic value and interpretation of faecal egg counts in sheep. New Zealand Veterinary Journal **29:** 129-132.

MEE, J. F., D. P. BERRY and A. R. CROMIE, 2011 Risk factors for calving assistance and dystocia in pasture-based Holstein–Friesian heifers and cows in Ireland. The Veterinary Journal **187:** 189-194.

MELLOR, D. J., 1983 Nutritional and placental determinants of fetal growth-rate in sheep and consequences for the newborn lamb. British Veterinary Journal **139:** 307-324.

MELLOR, D. J., 1988 Integration of perinatal events, pathophysiological changes and consequences for the newborn lamb. British Veterinary Journal **144:** 552-569.

MELLOR, D. J., and F. COCKBURN, 1986 A comparison of energy-metabolism in the newborn infant, piglet and lamb. Quarterly Journal of Experimental Physiology and Cognate Medical Sciences **71:** 361-379.

MELLOR, D. J., and K. J. STAFFORD, 2003 Assessing the welfare status of newborn farm animals. Animal Welfare **12:** 695-698.

MELLOR, D. J., and K. J. STAFFORD, 2004 Animal welfare implications of neonatal mortality and morbidity in farm animals. The Veterinary Journal **168:** 118-133.

MIRZA, S. N., and F. D. PROVENZA, 1992 Effects of age and conditions of exposure on maternally mediated food selection by lambs. Applied Animal Behaviour Science **33:** 35-42.

MITLOEHNER, F., J. MORROW-TESCH, S. WILSON, J. DAILEY and J. MCGLONE, 2001 Behavioral sampling techniques for feedlot cattle. Journal of Animal Science **79:** 1189-1193.

MORRIS, C. A., S. M. HICKEY and S. E. CLARKE, 2000 Genetic and environmental factors affecting lamb survival at birth and through to weaning. New Zealand Journal of Agricultural Research **43:** 515-524.

MORRIS, C. A., M. WHEELER, T. G. WATSON, B. C. HOSKING and D. M. LEATHWICK, 2005 Direct and correlated responses to selection for high or low faecal nematode egg count in Perendale sheep. New Zealand Journal of Agricultural Research **48:** 1-10.

MOUSSEAU, T. A., and D. A. ROFF, 1987 Natural selection and the heritability of fitness components. Heredity **59:** 181-197.

MUGGLI, N. E., W. D. HOHENBOKEN, L. V. CUNDIFF and K. W. KELLEY, 1984 Inheritance of Maternal Immunoglobulin G1 Concentration by the Bovine Neonate. J. Anim Sci. **59:** 39-48.

MUNOZ, C., A. F. CARSON, M. A. MCCOY, L. E. R. DAWSON, N. E. O'CONNELL *et al.*, 2008 Nutritional status of adult ewes during early and mid-pregnancy. 2. Effects of supplementation with selenised yeast on ewe reproduction and offspring performance to weaning. Animal **2:** 64-72.

NAWAZ, M., and H. H. MEYER, 1992 Performance of Polypal, Coopworth, and crossbred ewes: 1. Reproduction and lamb production. Journal of Animal Science **70:** 62-69.

NEWTON, K. G., J. C. L. HARRISON and A. M. WAUTERS, 1978 Sources of Psychrotrophic Bacteria on Meat at the Abattoir. Journal of Applied Microbiology **45:** 75-82.

NIEUWHOF, G. J., and S. C. BISHOP, 2005 Costs of the major endemic diseases of sheep in Great Britain and the potential benefits of reduction in disease impact. Animal Science **81:** 23-29.

NOLDUS, L. P. J. J., R. J. H. TRIENES, A. H. M. HENDRIKSEN, H. JANSEN and R. G. JANSEN, 2000 The Observer Video-Pro: New software for the collection, management, and presentation of time-structured data from videotapes and digital media files. Behavior Research Methods Instruments & Computers **32:** 197-206.

NORMAN, L. M., W. D. HOHENBOKEN and K. W. KELLEY, 1981 Genetic Differences in Concentration of Immunoglobulins G1 and M in Serum and Colostrum of Cows and in Serum of Neonatal Calves. J. Anim Sci. **53:** 1465-1472.

NOTTLE, M. B., D. O. KLEEMANN, V. M. HOCKING, T. I. GROSSER and R. F. SEAMARK, 1998 Development of a nutritional strategy for increasing lamb survival in Merino ewes mated in late spring/early summer. Animal Reproduction Science **52:** 213-219.

NOWAK, R., 1996 Neonatal survival: contributions from behavioural studies in sheep. Applied Animal Behaviour Science **49:** 61-72.

NOWAK, R., G. BRETON and E. MELLOT, 2001 CCK and development of mother preference in sheep: a neonatal time course study. Peptides **22:** 1309-1316.

NOWAK, R., M. KELLER, D. VAL-LAILLET and F. LÈVY, 2007 Perinatal visceral events and brain mechanisms involved in the development of mother–young bonding in sheep. Hormones and Behavior **52:** 92-98.

NOWAK, R., T. M. MURPHY, D. R. LINDSAY, P. ALSTER, R. ANDERSSON *et al.*, 1997 Development of a preferential relationship with the mother by the newborn lamb: Importance of the sucking activity. Physiology & Behavior **62:** 681-688.

NOWAK, R., and P. POINDRON, 2006 From birth to colostrum: early steps leading to lamb survival. Reproduction Nutrition Development **46** 431-446.

NOWAK, R., P. POINDRON and I. G. PUTU, 1989 Development of mother discrimination by single and multiple newborn lambs. Developmental Psychobiology **22:** 833-845.

NOWAK, R., P. POINDRON, F. SEBE, K. W. HART, A. CHADWICK *et al.*, 2006 Divergent selection on temperament affect vocal and locomotor activity in isolated lambs, pp. Short communication 45 in *Australian Society of Animal Production 26th Biennial Conference*

NOWAK, R., R. H. PORTER, F. LÈVY, P. ORGEUR and B. SCHAAL, 2000 Role of mother–young interactions in the survival of offspring in domestic mammals. Reviews of Reproduction **5:** 153-163.

NSOSO, S. J., M. J. YOUNG and P. R. BEATSON, 2000 A review of carcass conformation in sheep: assessment, genetic control and development. Small Ruminant Research **35:** 89-96.

O'CONNOR, C. E., N. P. JAY, A. M. NICOL and P. R. BEATSON, 1985 Ewe maternal behaviour score and lamb survival. Proceedings of the New Zealand Society of Animal Production **45:** 159-162.

O'CONNOR, C. E., and A. B. LAWRENCE, 1992 Relationship between lamb vigour and ewe behaviour at parturition. Animal Production **54:** 361-366.

O'CONNOR, C. E., A. B. LAWRENCE and D. G. M. WOOD-GUSH, 1992 Influence of litter size and parity on maternal behaviour at parturition in Scottish Blackface sheep. Applied Animal Behaviour Science **33:** 345-355.

O'RIORDAN, E. G., and J. P. HANRAHAN, 1992 The Effects of Sex and Castration on Growth Rate and Carcass Traits of Lambs. Irish Journal of Agricultural and Food Research **31:** 157-162.

OWENS, J. L., B. M. BINDON, T. N. EDEY and L. R. PIPER, 1985 Behaviour at parturition and lamb survival of Booroola Merino sheep. Livestock Production Science **13:** 359-372.

PAYNE, R. W., D. A. MURRAY, S. A. HARDING, D. B. BAIRD and D. M. SOUTAR, 2008 GenStat for Windows (11th Edition) Introduction., pp. VSN International,, Hemel Hempstead.

PEETERS, R., G. KOX and J. VAN ISTERDAEL, 1996 Environmental and maternal effects on early postnatal growth of lambs of different genotypes. Small Ruminant Research **19:** 45-53.

PFEFFER, A., R. J. SHAW, R. S. GREEN and M. D. PHEGAN, 2005 The transfer of maternal IgE and other immunoglobulins specific for *Trichostrongylus colubriformis* larval excretory/secretory product to the neonatal lamb. Veterinary Immunology and Immunopathology **108:** 315-323.

POINDRON, P., R. SOTO and A. ROMEYER, 1997 Decrease of response to social separation in preparturient ewes. Behavioural Processes **40:** 45-51.

POLLARD, J. C., 2006 Shelter for lambing sheep in New Zealand: a review. New Zealand Journal of Agricultural Research **49:** 395-404.

PRICE, T., and D. SCHLUTER, 1991 On the low heritability of life-history traits. Evolution **45:** 853-861.

PURVIS, I. W., and M. HILLARD, 1997 Biology and genetics of reproduction, pp. 375-394 in *The Genetics of Sheep*, edited by L. R. PIPER and A. RUVINSKY. CAB, New York.

RANSOM, K. P., and P. D. MULLANEY, 1976 Effects of sex and some environmental factors on weaning weight in sheep. Australian Journal of Experimental Agriculture **16:** 19-23.

RAO, S., and D. R. NOTTER, 2000 Genetic analysis of litter size in Targhee, Suffolk, and Polypay sheep. Journal of Animal Science **78:** 2113-2120.

REES, S., C. MALLARD, S. BREEN, M. STRINGER, M. COCK *et al.*, 1998 Fetal brain injury following prolonged hypoxemia and placental insufficiency: A review. Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology **119:** 653-660.

RILEY, D. G., C. C. CHASE, T. A. OLSON, S. W. COLEMAN and A. C. HAMMOND, 2004 Genetic and nongenetic influences on vigor at birth and preweaning mortality of purebred and high percentage Brahman calves. Journal of Animal Science **82:** 1581-1588.

RIUS-VILARRASA, E., L. BUNGER, S. BROTHERSTONE, J. M. MACFARLANE, N. R. LAMBE *et al.*, 2010 Genetic parameters for carcass dimensional measurements from Video Image Analysis and their association with conformation and fat class scores. Livestock Science **128:** 92-100.

ROBERTSON, S. M., M. A. FRIEND, J. C. BROSTER and B. J. KING, 2011 Survival of twin lambs is increased with shrub belts. Animal Production Science **51:** 925-938.

ROBINSON, J. J., T. G. MCEVOY and J. D. SINCLAIR, 1999 Nutritional effects on foetal growth. Animal Science **68:** 325-331.

ROBINSON, J. J., J. A. ROOKE and T. G. MCEVOY, 2002 *Nutrition for conception and pregnancy*. CABI Publishing, Wallingford, Oxon, OX10 8DE, UK; CSIRO Publishing, 150 Oxford Street, P. O. Box 1139, Collingwood, VIC, 3066, Australia.

RODEN, J., and W. HARESIGN, 2008 A comparison of the performance of New Zealand Suffolks with UK Suffolks in a Welsh lowland environment, pp. 23. date accessed December 2008. http://www.hccmpw.org.uk/medialibrary/publications/suffolk%2020project%2020FINAL%2020REPORT%2005B2001%2005D.pdf. Aberystwyth University, Aberystwyth.

ROFF, D. A., 1997 *Evolutionary quantitative genetics*. Academic Press, London.

ROOKE, J. A., C. M. DWYER and C. J. ASHWORTH, 2008 The potential for improving physiological, behavioural and immunological responses in the neonatal lamb by trace element and vitamin supplementation of the ewe. Animal **2:** 514-524.

ROOKE, J. A., J. G. M. HOUDIJK, K. MCILVANEY, C. J. ASHWORTH and C. DWYER, 2010 Differential effects of maternal undernutrition between days 1 and 90 of pregnancy on ewe and lamb performance and lamb parasitism in hill or lowland breeds. Journal of Animal Science **88:** 3833-3842.

ROOKE, J. A., S. MATHESON, S. ISON, M. JACK, C. J. ASHWORTH *et al.*, 2009 The effect of late pregnancy supplementation of ewes with vitamin E on lamb vigour. Animal **3:** 1555-1561.

ROOKE, J. A., A. G. SINCLAIR and S. A. EDWARDS, 2001a Feeding tuna oil to the sow at different times during pregnancy has different effects on piglet long-chain polyunsaturated fatty acid composition at birth and subsequent growth. British Journal of Nutrition **86:** 21-30.

ROOKE, J. A., A. G. SINCLAIR and M. EWEN, 2001b Changes in piglet tissue composition at birth in response to increasing maternal intake of long-chain n-3 polyunsaturated fatty acids are non-linear. British Journal of Nutrition **86:** 461-470.

ROSATI, A., E. MOUSA, L. D. VAN VLECK and L. D. YOUNG, 2002 Genetic parameters of reproductive traits in sheep. Small Ruminent Research **43:** 65–74.

SAFARI, E., N. M. FOGARTY and A. R. GILMOUR, 2005 A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. Livestock Production Science **92:** 271-289.

SARGISON, N., 2004 Differential diagnosis of diarrhoea in lambs. In Practice **26:** 20-27.

SAWALHA, R. M., J. CONINGTON, S. BROTHERSTONE and B. VILLANUAVA, 2007 Analyses of lamb survival of Scottish Blackface sheep. Animal **1:** 151-157.

SAWYER, M., C. H. WILLADSEN, B. I. OSBURN and T. C. MCGUIRE, 1977 Passive transfer of colostral immunoglobulins from ewe to lamb and its influence on neonatal lamb mortality. Journal of the American Veterinary Medical Association **171:** 1255-1259.

SCOTT, P. R., 2005 The management and welfare of some common ovine obstetrical problems in the United Kingdom. The Veterinary Journal **170:** 33-40.

SHELTON, M., 1964 Relation of Birth Weight to Death Losses and to Certain Productive Characters of Fall-Born Lambs. Journal of Animal Science **23:** 355-359.

SHNIDER, S. M., R. G. WRIGHT, G. LEVINSON, M. F. ROIZEN, K. L. WALLIS *et al.*, 1979 Uterine blood flow and plasma norepinephrine changes during maternal stress in the pregnant ewe. Anesthesiology **50:** 524-527.

SIMM, G., 1998 *Genetic improvement of cattle and sheep*. Farming Press, Tunbridge, UK.

SIMM, G., R. M. LEWIS, J. E. COLLINS and G. J. NIEUWHOF, 2001 Use of sire referencing schemes to select for improved carcass composition in sheep. Journal of Animal Science **79:** E255-259.

SLEE, J., and A. SPRINGBETT, 1986 Early post-natal behaviour in lambs of ten breeds. Applied Animal Behaviour Science **15:** 229-240.

SMITH, G. M., 1977 Factors affecting birth weight, dystocia and preweaning survival in sheep. Journal of Animal Science **44:** 745-753.

SNOWDER, D. G., 2002 Composite trait selection for improving lamb production. Sheep & Goat Research **17:** 42-49.

SNOWDER, D. G., 2008 Genetic improvement of overall reproductive success in sheep: A review. Associacion Latinoamericana de Produccion Animal **16:** 32-40.

SNOWDER, G. D., A. D. KNIGHT, L. D. VAN VLECK, C. M. BROMLEY and T. R. KELLOM, 2001 Usefulness of subjective ovine milk scores: I. Associations with range ewe characteristics and lamb production. Journal of Animal Science **79:** 811-818.

SPEAR-SMITH, J., J. F. BRIEN, M. GRAFE, R. ALLRICH and J. D. REYNOLDS, 2000 Chronic ethanol exposure during late gestation produces behavioral anomalies in neonatal lambs. Neurotoxicology and Teratology **22:** 205-212.

SPEIJERS, M. H. M., A. F. CARSON, L. E. R. DAWSON, D. IRWIN and A. W. GORDON, 2010 Effects of sire breed on ewe dystocia, lamb survival and weaned lamb output in hill sheep systems. Animal **4:** 486-496.

STEAR, M. J., and S. C. BISHOP, 1996 The key componants of resistance to *Ostertagia circurncincta* in lambs. Parasitology Today **12:** 438-441.

STEAR, M. J., S. MITCHELL, S. STRAIN, S. C. BISHOP and Q. A. MCKELLAR, 2000 The influence of age on the variation among sheep in susceptibility to natural nematode infection. Veterinary Parasitology **89:** 31–36.

STEARNS, S. C., 1992 *The Evolution of Life histories*. Oxford University Press, Oxford, New York.

STEVENS, D., G. ALEXANDER, B. MOTTERSHEAD and J. J. LYNCH, 1984 Role of the lamb in post-partum separation of ewes from twin lambs, pp. 15:751 in *Proceedings of the Australian Society of Animal Production*.

STIRLING, D. G., D. RÉALE and D. A. ROFF, 2002 Selection, structure and the heritability of behaviour. Journal of Evolutionary Biology **15:** 277-289.

STIRLING, G., D. J. FAIRBAIRN, S. JENSEN and D. A. ROFF, 2001 Does a negative genetic correlation between wing morph and early fecundity imply a functional constraint in Gryllus firmus? Evolutionary Ecology Research **3:** 157-177.

TELLAM, R. L., and V. M. BOWLES, 1997 Control of blowfly strike in sheep: Current strategies and future prospects. International Journal for Parasitology **27:** 261-273.

TUCHSCHERER, M., B. PUPPE, A. TUCHSCHERER and U. TIEMANN, 2000 Early identification of neonates at risk: Traits of newborn piglets with respect to survival. Theriogenology **54:** 371-388.

VAL-LAILLET, D., M. MEURISSE, Y. TILLET and R. NOWAK, 2009 Behavioural and neurobiological effects of colostrum ingestion in the newborn lamb associated with filial bonding. European Journal of Neuroscience **30:** 639-650.

VAL-LAILLET, D., M. SIMON and R. NOWAK, 2004 A full belly and colostrum: two major determinants of filial love. Developmental Psychobiology **45:** 163-173.

VINCE, M. A., 1993 Newborn lambs and their dams - the interaction that leads to sucking, pp. 239-268 in *Advances in the Study of Behavior, Vol 22*. Academic Press Inc, San Diego.

VUKAVIC, T., 1984 Timing of the gut closure. Journal of Pediatric Gastroenterology and Nutrition **3:** 700-703.

VULICH, S. A., E. G. ORIORDAN and J. P. HANRAHAN, 1991 Effect of litter size on herbage intake at pasture by ewes and their progeny. Animal Production **53:** 191-197.

WALLING, G. A., P. M. VISSCHER, A. D. WILSON, B. L. MCTEIR, G. SIMM *et al.*, 2004 Mapping of quantitative trait loci for growth and carcass traits in commercial sheep populations. Journal of Animal Science **82:** 2234-2245.

WASSMUTH, R., A. LÖER and H.-J. LANGHOLZ, 2001 Vigour of lambs newly born to outdoor wintering ewes. Animal Science **72:** 169-178.

WATERHOUSE, A., 1996 Animal welfare and sustainability of production under extensive conditions—A European perspective. Applied Animal Behaviour Science **49:** 29-40.

WEISS, D. J., 1986 The discriminating power of ordinal data. Journal of Social Behavior & Personality, **1:** 381-389.

WILSON, A. J., D. RÉALE, M. N. CLEMENTS, M. M. MORRISSEY, E. POSTMA *et al.*, 2010 An ecologist's guide to the animal model. Journal of Animal Ecology **79:** 13-26.

WOOLASTON, R. R., and R. L. BAKER, 1996 Prospects of Breeding Small Ruminants for Resistance to Internal Parasites. International Journal for Parasitology **26:** 845-855.

YAPI, C. V., W. J. BOYLAN and R. A. ROBINSON, 1992 Heritability and repeatability estimates and correlations of lamb mortality with birth weight and litter size. World Review of Animal Production **27:** 55-60.